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### A review of the natural enemies of beetles in the subtribe Diabroticina (Coleoptera: Chrysomelidae): implications for sustainable pest management

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## REVIEW

### A review of the natural enemies of beetles in the subtribe *Diabroticina* (Coleoptera: Chrysomelidae): implications for sustainable pest management

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*Diabroticina* is a speciose subtribe of New World Chrysomelidae (Subfamily Galerucinae: Tribe Luperini) that includes pests such as corn rootworms, cucumber beetles and bean leaf beetles (e.g. *Diabrotica*, *Acalymma*, *Cerotoma* species). The evolution and spread of pesticide resistance, the European invasion of *Diabrotica v. virgifera* LeConte, and possible development of resistance due to the large-scale deployment of *Diabrotica*-active *Bt* maize in North America have generated a sense of urgency in developing biological control options against *Diabroticina* pests. In the present study, we review available knowledge on biological control options, including 290 publications on natural enemy–*Diabroticina* associations in the New World. Several natural enemy species or groups appear to be promising candidates for control strategies with different ecological rationales. We propose that future research should pursue: (1) development of inundative biological control products, particularly mass-produced entomopathogenic nematodes and fungi, (2) understanding of specific natural enemies of *Diabroticina* larvae throughout the Americas and of adults particularly in higher altitudes of Central America or northern South America including potential classical biological control agents against *D. v. virgifera*; (3) enhancement of natural enemies through cultural practices, i.e. reduced tillage, reduced weed control, cover crops, diversified crop rotations or soil amendments. Research and action must be coordinated to accelerate the exploration of biological control options.

**Keywords:** inundative; classical; conservation biological control; *Diabrotica*; *Acalymma*; *Cerotoma*

## Introduction

The *Diabroticina* constitute a subtribe of chrysomelid beetles (Subfamily Galerucinae: Tribe Luperini) and includes three major pest genera: *Acalymma* Barber

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(Section Diabroticites), *Cerotoma* Chevrolat (Section Cerotomites), and *Diabrotica* Chevrolat (Section Diabroticites) (Gillespie, Tallamy, Riley, and Cognato 2008). All three genera are endemic to the New World (Jolivet and Verma 2002).

The ca. 350 described species of *Diabrotica* are divided into three series: *virgifera*, *fucata* and *signifera*. The pest species in this genus belong to either the *virgifera* group, which feeds on grasses (Poaceae), or the *fucata* group, which is more polyphagous (Krysan and Smith 1987). The northern corn rootworm, *D. barberi* Smith Lawrence as well as *Diabrotica virgifera*, including the two subspecies: the western corn rootworm, *D. virgifera virgifera* LeConte, and the Mexican corn rootworm, *D. v. zea* Krysan and Smith, make up the corn rootworm complex: a group within the *virgifera* group whose larvae feed primarily on maize roots, *Zea mays* (L.) (Chiang 1973; Moeser and Vidal 2005). The subspecies *D. v. virgifera* probably originated in Mexico or Central America (Branson and Krysan 1981; Krysan and Smith 1987), becoming a major pest in the USA and Canada as maize-growing areas expanded northwards during the twentieth century (Levine and Oloumi-Sadeghi 1991; Kim and Sappington 2005). Between the late 1980s and early 2000s, *D. v. virgifera* was accidentally introduced several times into Europe (Kiss et al. 2005; Miller et al. 2005), and threatens to be as troublesome as it is in North America (Baufeld and Enzian 2005). Two North American *Diabrotica* species in the *fucata* group are also pests of many horticultural and field crops, including cucurbits, peanuts, sweet potatoes, leafy vegetables and flowers: the banded cucumber beetle, *Diabrotica balteata* LeConte, and spotted cucumber beetles, *Diabrotica undecimpunctata* (= *12-punctata*) Mannerheim. *Diabrotica undecimpunctata* is a wide-ranging species with four described subspecies, including the southern corn rootworm or spotted cucumber beetle, *D. u. howardi* Barber and the western spotted cucumber beetle, *D. u. undecimpunctata* Mannerheim, (Krysan 1986; Jolivet and Verma 2002). South American *Diabrotica* species include the widespread pests *D. speciosa* (Germar) (*fucata* group) and *D. viridula* (F.) (*virgifera* group).

Members of the genus *Acalymma*, which comprises more than 70 species, are mainly specialised herbivores of Cucurbitaceae. Foliage-feeding by adults can significantly damage young plants, and root-feeding by larvae impairs root development (Brewer, Story, and Wright 1987; Ellers-Kirk, Fleischer, Snyder, and Lynch 2000). *Acalymma albidovittata* (Baly), *A. bivittula* (Kirsch) and *A. bruchii* (Bowditch) are serious pests of cucurbit crops in subtropical and tropical South America. In North America, the genus is represented by two pest species: the western striped cucumber beetle *Acalymma trivittatum* (= *trivittata*) (Mannerheim), and the striped cucumber beetle *Acalymma vittatum* (= *vittata*) (F.) a known vector of the important bacterial wilt agent *Erwinia tracheiphila* Holland (Enterobacteriales: Enterobacteriaceae) (Fleischer, de Mackiewicz, Gildow, and Lukezic 1999). Together, the cucumber beetles *A. vittatum* and *D. undecimpunctata* are the most severe pests in organic cucurbit production in the USA (Walz 1999).

The genus *Cerotoma* comprises 18 species, including two pests: the bean leaf beetle *C. trifurcata* (Forster) in North America (Lundgren and Riedell 2008), and *C. arcuata* Olivier (= *Andrector arcuatus*) in South America (Teixeira, Coutinho, and Franco 1996). Both species are primarily pests on beans, but occasionally also on cucurbits and other plants (Kogan, Waldbauer, Boiteau, and Eastman 1980; Nava and Postali Parra 2003).

Enormous amounts of insecticides are released into the environment during efforts to suppress *Diabroticina* pests. For example, in North America, 7.6 million hectares of maize were treated with soil insecticides in 2005 (NASS 2006), a number which has recently increased dramatically with the widespread adoption of insecticide-treated seeds. Economic analyses estimated that the combined costs of controlling *Diabrotica* pests in maize and yield loss, are about \$1.17 billion per annum (Chandler 2003; P. Mitchell, 2005, personal communication). Maize crop protection in North America and Europe are still fundamentally different based on the large scale use of transgenic maize in North America. In Europe, farmers have started to use soil insecticides, insecticide-coated seeds and also foliar insecticides to control *D. v. virgifera* since its introduction (Zsoller Hatala et al. 2006). Foliar insecticides threaten current biological control systems, such as release of *Trichogramma* wasps (Hymenoptera: Trichogrammatidae) to control lepidopteran pests, like *Ostrinia nubilalis* (Lepidoptera: Pyralidae) (Babendreier et al. 2006).

Although crop rotation and chemical control have been the primary management strategies for *Diabroticina* (Levine and Oloumi-Sadeghi 1991), the beetles have repeatedly evolved resistant behaviours and physiologies (Meinke, Siegfried, Wright, and Chandler 1998; Wright et al. 2000; Ward et al. 2005). Several *Diabroticina* pest species have been reported to be resistant to cyclodienes (Ball and Weekman 1963), methyl-parathion, or carbaryl (Meinke et al. 1998). Furthermore, high rates of methyl-parathion resistance among *Diabrotica* spp. subsisted in some areas even after the selection pressure was removed (Parimi, Scharf, Meinke, Chandler, and Siegfried 2003). Until recently, crop rotation between maize and soybeans in much of the Corn Belt in the eastern USA succeeded in making *Diabrotica*-targeted insecticide applications to first-year maize unnecessary. In areas of Indiana and Illinois, however, *D. v. virgifera* has overcome crop rotation strategies through novel oviposition behaviour, which is spreading (Onstad et al. 1999; Onstad, Spencer, Guse, Levine, and Isard 2001b; O'Neal, Difonzo, Landis, and Meek 2002; Isard, Spencer, Mabry, and Levine 2004). Since extended egg diapause was documented in *D. barberi* (Krysan, Jackson, and Lew 1984), eggs of *D. v. virgifera* were also thought to have extended diapause, remaining unhatched until the end of soybean rotations and explaining novel first-year maize damage (Fischer, Jackson, and Lew 1994). However, it is now known that *D. v. virgifera* displays the adaptive behaviour of leaving maize to feed and oviposit in other crops, like soybean (Sammons, Edwards, Bledsoe, Boeve, and Stuart 1997; Rondon and Gray 2004). Thus, first year maize is planted in soil infested beforehand with *D. v. virgifera* eggs, renewing the requirement for soil and foliar insecticides to prevent damage. Deployment of transgenic *Bt* maize in the USA since the early 2000s (Ward et al. 2005) has raised concerns that *Diabrotica* species will develop resistance and overcome this control strategy as well (Onstad, Guse, Spencer, Levine, and Gray 2001a; Crowder and Onstad 2005; Siegfried, Vaughn, and Spencer 2005).

The expansion and adaptability of *Diabroticina* pests and the lack of sustainable control strategies, have generated a sense of urgency among scientists. The development of biological control options against *Diabrotica* species is especially important. Three main categories of biological control are recognized: (1) classical biological control, (2) augmentation through inoculative or inundative control, and (3) natural enemy conservation (Hajek 2004).

Much has been clarified about Diabroticina and their natural enemies since the review by Kuhlmann and van der Burgt (1998). In this review, we include current findings, particularly relating to natural enemy–Diabroticina associations in the New World, and their implications for biological control.

## Review

### Microbials

Diabroticina beetles are susceptible to infection by a broad range of microbial agents including viruses, bacteria and fungi (Tanada and Kaya 1993; Boucias and Pendland 1998; Kuhlmann and van der Burgt 1998). These infectious agents vary in pathogenicity from those causing chronic infections with subtle impacts on host physiology, like *Wolbachia* bacteria (Rickettsiaceae), to very virulent pathogens that cause rapid mortality, like *Metarhizium* fungi (Hypocreales) (Degrugillier, Degrugillier, and Jackson 1991; Pilz, Wegensteiner, and Keller 2008).

Pathogens generally, and viral and protista agents in particular, are relatively host specific, infecting only a few related host species. Bacterial and fungal species, however, tend to have broader ranges, infecting host species in different families or even different orders, although individual isolates may be very specific. Nevertheless, microbials have the potential to be developed as control products which are more target-specific and effective than insecticides. Because of their specificity, microbials are often compatible with other biological control strategies and can be incorporated into integrated pest management (IPM) systems (Sudakin 2003). The suitability of a microbe for a particular biological control strategy depends on its infectivity, virulence and persistence.

### Fungi

Entomopathogenic fungi have been developed and used against a broad range of insect pests, including beetles (Goettel, Ellenberg, and Glare 2005). Numerous products are registered, mostly for use in greenhouses but these include several for soil dwelling pests, e.g. *Beauveria brongniartii* (Sac) Petch (Hypocreales: Cordycipitaceae) against the European cockchafer *Melolontha melolontha* (Coleoptera: Scarabaeidae), and *Metarhizium anisopliae* (Metsch.) Sorokin (Hypocreales: Clavicipitaceae) against the greyback cane grub *Dermolepida albohirtum* (Coleoptera: Scarabaeidae) (Keller, Schweizer, Keller, and Brenner 1997; Copping 2004).

Although arable soils are rich in entomopathogenic fungi (Strasser, Hutwimmer, and Zelger 2006), and Diabroticina are often found infected by these organisms (Table 1), the role of entomopathogenic fungi in population suppression of Diabroticina pests is still largely unknown. In the Americas, *Metarhizium*, *Paecilomyces*, *Laboulbenia*, and *Beauveria* species are natural pathogens of Diabroticina species (Table 1). In extensive surveys, Bruck and Lewis (2001) estimated that up to 3% of adult *Diabrotica* beetles collected in maize fields in central Iowa are infected with *Beauveria bassiana* (Bals.) Vuill. (Hypocreales: Cordycipitaceae). In Brazil, Heineck-Leonel and Salles (1997) reported that up to 14% of field-collected adults of *D. speciosa* are infected by *B. bassiana* and 6% by *M. anisopliae*. However, in both of the above studies, the beetles were held under laboratory conditions after

Table 1. Records of entomopathogenic fungi, including microsporidia, attacking species in the subtribe Diabroticina (Coleoptera: Chrysomelidae). Names of strains are presented in capital letters. The taxonomy classification refers to Sung *et al.* (2007) and Luangsa *et al.* (2005).

Host	Pathogen	Order: Family	Stage attacked	Location	Reference
<i>Acalymma blomorum</i> Munroe Smith	<i>Beauveria bassiana</i> (Bals.) Vuill. <i>Laboulbenia diabroticae</i> (Thaxt.)	Hypocreales: Cordycipitaceae Laboulbeniales: Laboulbeniaceae	adult adult	Mexico Mexico	Eben & Barbercheck 1996 Tavares 1985; Eben and Barbercheck 1996
<i>A. bivittula</i> (Kirsch)	<i>B. bassiana</i>		adult	Brazil	Dequech 2006
<i>A. fairmairei</i> (F.)	<i>L. diabroticae</i>		adult	Mexico	Tavares 1985; Eben & Barbercheck 1996
<i>Cerotoma arcuata</i> Olivier (= <i>Andrector arcuatus</i> )	<i>Aspergillus</i> sp.***  <i>B. bassiana</i>  <i>B. bassiana</i> ** <i>B. bassiana</i> CP5 <i>B. bassiana</i> CG156, CG213 <i>Zoophthora radicans</i> (Brefeld) Batko <i>Metarhizium anisopliae</i> (Metsch.) Sorok. CG210, CG321	Eurotiales: Trichocomaceae    Entomophthorales: Entomophthoraceae Hypocreales: Clavicipitaceae	adult*** adult adult adult larva unknown larva	Lab Brazil Brazil** Lab Lab Unknown Lab	Lord et al. 1987 Humber & Hansen 2005; Yaginuma 1994; Anonymous 2007 Magalhaes et al. 1986 Lord et al. 1987 Teixeira & Franco 2007 Anonymous 2007 Teixeira et al. 2007
<i>C. trifurcata</i> (Forster)	<i>Aspergillus</i> sp.***  <i>B. bassiana</i>  <i>B. bassiana</i> <i>M. anisopliae</i>		overwintering adult*** overwintering adult adult overwintering adult	USA USA USA Lab USA	Payah & Boethel 1986; Marrone et al. 1983 Payah & Boethel 1986; Marrone et al. 1983 Day 1986 Payah & Boethel 198.; Marrone et al. 1983

Table 1 (Continued)

Host	Pathogen	Order: Family	Stage attacked	Location	Reference
<i>Cerotoma</i> sp.	<i>Paecilomyces</i> sp.	Eurotiales: Trichocomaceae	overwintering adult	USA	Payah & Boethel 1986
	two unidentified Microsporidia species	Microsporida	adult	USA	Marrone et al. 1983
	<i>B. bassiana</i>		adult	Brazil	Daoust & Pereira 1986, Humber & Hansen 2005
	<i>Paecilomyces lilacinus</i> (Thom) Samson CG301		egg	Brazil	Tigano-Milani et al. 1995
<i>Diabrotica amecameca</i> Krysan Smith	<i>B. bassiana</i>		adult	Mexico	Eben, 2002
<i>D. balteata</i> LeConte	<i>B. bassiana</i>		adult	Mexico	Garcia-Gutierrez et al. 1999; Humber & Hansen 2005
<i>D. barberi</i> Smith Lawrence	<i>Metarhizium</i> sp.		larva, pupa, adult	Lab	Saba 1970
	<i>B. bassiana</i>		adult	Lab	Humber & Hansen 2005
	<i>B. bassiana</i>		adult	USA	Day 1986
	<i>B. bassiana</i> AACC-012-90, BB8303R3		adult	Lab	Day 1986
<i>D. longicornis</i> (Say) <i>D. speciosa</i> (Germar)	<i>Tarichium</i> sp.	Entomophthorales: Entomophthoraceae	adult	USA	Naranjo & Steinkraus 1988
	<i>B. bassiana</i>		adult	Lab	Branson et al. 1975
	<i>B. bassiana</i>		adult	Brazil, Argentina	Daoust & Pereira 1986; Humbert & Hansen 2005; Dequech 2006; Hohmann 1989
	<i>B. bassiana</i> **		adult	Brazil**	Pianoski et al. 1990
	<i>B. bassiana</i>		adult	Brazil	Heineck-Leonel & Salles 1997

Table 1 (Continued)

Host	Pathogen	Order: Family	Stage attacked	Location	Reference
<i>D. undecimpunctata</i> (= <i>I2-punctata</i> ) Mannerheim	<i>B. bassiana</i> FHD13	Hypocreales: Cordycipitaceae	larva	Lab	Consolo et al. 2003
	<i>B. bassiana</i> CNPSO-BB467		adult	Brazil	Micheli 2005
	<i>B. bassiana</i> CNPSO-B59 and 61		adult	Lab	Micheli 2005
	<i>M. anisopliae</i>		adult	Brazil	Humber & Hansen 2005; Heineck-Leonel & Salles 1997
	<i>M. anisopliae</i> CG293		larva	Lab	Silva-Werneck & Faria 1995
	<i>Isaria fumosorosea</i> Wize 5 CG STRAINS		egg	Lab	Tigano-Milani et al. 1995
	<i>P. lilacinus</i> 10 CG STRAINS		egg	Lab	Tigano-Milani et al. 1995
	<i>B. bassiana</i>		adult	USA	Humber & Hansen 2005
	<i>B. bassiana</i> **		larva	USA**	Krueger & Roberts 1997
	<i>B. bassiana</i>		adult	USA	Rockwood & Chamberlin 1943
	<i>B. bassiana</i>		adult	Lab	Day 1986
	<i>M. anisopliae</i> BIO1020		larva	Lab	Zimmermann & Baltruschat 1991
<i>D. u. howardi</i> Barber	<i>M. anisopliae</i> **		larva	USA**	Krueger & Roberts 1997
	<i>B. bassiana</i>		adult	Lab	Branson et al. 1975
			adult	USA	Brooks & Raun 1965
<i>D. virgifera</i> LeConte	<i>M. anisopliae</i>		egg, larva	Lab	Tallamy et al. 1998
	<i>B. bassiana</i>		adult	Mexico, Lab	Humber & Hansen 2005; Branson et al. 1975
			adult	USA	Brooks & Raun 1965
<i>D. v. virgifera</i> LeConte	<i>Arthrobotrys</i> sp.	Orbiliales: Orbiliaceae	egg	Lab	Oloumi-Sadeghi & Levine 1989
	<i>B. bassiana</i>		adult	Lab	Mulock & Chandler, 2000; 2001a; b
	<i>B. bassiana</i> AACC-012-90, BB8303R3		adult	Lab	Day 1986
	<i>B. bassiana</i> **		adult	USA**	Bruck & Lewis 2002



Table 1 (Continued)

Host	Pathogen	Order: Family	Stage attacked	Location	Reference
	<i>B. bassiana</i>		adult	Mexico	Alvarez-Zagoya & Perez-Dominguez 2006
	<i>B. bassiana</i>		adult	Hungary	Toepfer & Kuhlmann 2004
	<i>Beauveria brongniartii</i> (Sacc.) Petch, BBR858	Hypocreales: Cordycipitaceae	larva, adult	Lab	Pilz et al. 2007
	<i>Beauveria</i> sp.		adult, pupa, larva	Hungary, Romania, Serbia	Pilz et al. 2008
	<i>Cylindrocarpon destructans</i> (Zins) Scholten	Hypocreales: Nectriaceae	egg	Lab	Oloumi-Sadeghi & Levine 1989
	<i>Fusarium oxysporum</i> Scl.	Hypocreales: Nectriaceae	egg	Lab	Oloumi-Sadeghi & Levine 1989
	<i>M. anisopliae</i>		adult	Hungary	Toepfer & Kuhlmann 2004
	<i>M. anisopliae</i>		adult, pupa, larva	Hungary, Romania, Serbia	Pilz et al. 2008
	<i>M. anisopliae</i> DIABROTICA V.V. STRAINS, MA2258, MA2062, BIPESCO5		larva, adult	Lab	Pilz et al. 2007
	<i>M. anisopliae</i> 3 AGRIOTES, MA2256,		adult	Lab	Pilz et al. 2007
	<i>M. anisopliae</i> MA5019		larva	Lab	Pilz et al. 2007
	<i>M. anisopliae</i> KOPPERT MA AKSET727, KOPPERT MA ITALY		adult	Lab	Zijlstra 1998
	<i>Paecilomyces lilacinus</i> (Thom) Samson	Eurotiales: Trichocomaceae	egg	Slovenia	Modic 2007; Modic et al. 2008
	<i>Clonostachys rosea</i> Link Fries	Hypocreales Bionectriaceae	egg	Slovenia	Modic 2007; Modic et al. 2008
	Unidentified Microsporidia	Microsporidia	adult	Lab	Jackson 1986

Table 1 (Continued)

Host	Pathogen	Order: Family	Stage attacked	Location	Reference
<i>D. viridula</i> (F.)	<i>L. diabroticae</i>		adult	Mexico	Tavares 1985; Eben & Barbercheck 1996
<i>Diabrotica</i> spp.	<i>B. bassiana</i>		adult	Brazil, Columbia	Humber & Hansen 2005; Maddox & Kinney 1989
			adult	USA	Bruck & Lewis 2001
	<i>M. anisopliae</i>		adult	Mexico	Garcia-Gutierrez et al. 1999
			adult	Brazil	Humber & Hansen 2005

\*\* denotes application of laboratory strains to the field  
\*\*\* mainly considered secondary or opportunistic pathogens (Lord et al. 1987)

collection; this experimental procedure can result in insects becoming infected subsequent to removal from the field (Goettel, Inglis, and Wraight 2000). Marrone, Brooks, and Stinner (1983) found that about 2% of overwintering adult *C. trifurcata* die from *B. bassiana* infections in North Carolina, USA. Naranjo and Steinkraus (1988) found that *D. barberi* cadavers collected from fields in New York State, USA were infected with an unidentified fungus (tentatively ascribed as a *Tarichium* species, Zygomycetes). In Mexico, *B. bassiana* as well as *Laboulbenia diabroticae* Thaxter (Laboulbeniales: Laboulbeniaceae) were found infecting several *Diabrotica* and *Acalymma* species (Eben and Barbercheck 1996; Eben 2002). Extensive surveys in central and south-eastern Europe indicated low levels of *B. bassiana* and *M. anisopliae* in *D. v. virgifera*, with less than 2% in larvae, about 0.2% in pupae, and less than 0.01% in adults (Toepfer and Kuhlmann 2004; Pilz et al. 2008).

Several fungal isolates that are highly virulent against Diabroticina, in particular against *D. speciosa* and *D. v. virgifera*, have been identified (Table 1). For instance, of seven isolates of *M. anisopliae* and nine isolates of *B. bassiana* screened, Consolo, Salerno, and Beron (2003) found 14 that were pathogenic to third instar *D. speciosa*, causing 5–70% mortality. Tonet and Reis (1979) achieved 100% mortality in adult *D. speciosa* following inoculation with *B. bassiana* conidia, including fungal application to insects or to foliage. Using similar bioassays, Pilz, Wegensteiner, and Keller (2007) achieved up to 50% mortality in *D. v. virgifera* larvae and up to 90% in adults by some of the 17 strains of *M. anisopliae* tested, while *B. bassiana* was generally less effective. Further, Mulock and Chandler (2001a) reported that early treatments of adults with *B. bassiana* result in a significant reduction in fecundity. They speculated that a properly timed application of the fungus could result in 75% mortality. They observed horizontal transmission from dead infected beetles, and suggested that secondary infections from sporulating cadavers could augment population reductions after fungi are applied (Mulock and Chandler 2001b).

Field applications of fungi for Diabroticina control were conducted and evaluated in South America, North America, and central Europe. Mulock and Chandler (2000) achieved a 50% reduction in adult populations of *D. v. virgifera* in field-cage studies following a single application of *B. bassiana* conidia. Kinney, Maddox, Dazey, and McKinnis (1989) applied *B. bassiana* conidia to the soil surface as an aqueous suspension and disked them 7–10 cm deep prior to planting maize at four locations in Illinois, USA for control of *Diabrotica* spp. larvae. The treatment resulted in reduced root damage only in 1 year out of 5, and in two locations out of four. Pianoski et al. (1990) tested *B. bassiana* strains in combination with fertilizer treatments for control of *D. speciosa* in bean crops under field and laboratory conditions in Brazil. In the field, *B. bassiana* had the strongest effect when plants were treated with excess nitrogen, but in laboratory trials, *B. bassiana* was most effective without fertilizers. Krueger and Roberts (1997) evaluated applications of large numbers of dried mycelia particles (9.3 g particles m<sup>-1</sup>) of *M. anisopliae* and *B. bassiana* for the control of *D. undecimpunctata* on maize in New York State, USA. Applications caused significant reductions in *D. undecimpunctata* emergence, root feeding and maize goose-necking. Two strains of *M. anisopliae* are being investigated for use in inundative biological control against *D. v. virgifera* in Europe using fungus barley grain formulations developed for other soil-dwelling pests (S. Keller, H. Strasser, Ch. Pilz, 2007, personal communication).

Microsporidia, recently included in the entomopathogenic fungi (McLaughlin, McLaughlin, and Lemke 2001), have been found in field-collected and laboratory-reared *Diabroticina* beetles (Table 1) (Marrone et al. 1983; Jackson 1986). However, the impact of microsporidia on *Diabroticina* pest populations in the field is unknown and needs further investigation (Levine and Oloumi-Sadeghi 1991).

### *Bacteria*

Although bacteria exploit a diversity of habitats and niches and employ a wide variety of metabolic strategies for growth and survival (Cowan and Liston 1977), only a few bacteria are currently used in controlling beetle pests. *Bacillus thuringiensis* Berliner (*Bt*) (Eubacteriales: Bacillaceae) is the most important bacterium in microbial pest management to date. This gram-positive, spore-forming bacterium produces several classes of insecticidal proteins including  $\delta$ -endotoxins which are highly specific insect-gut toxins active against Lepidoptera, Coleoptera, and Diptera (Bravo, Soberón, and Gill 2005). *Bacillus thuringiensis* insecticidal proteins are delivered to insects most often in formulated products (such as suspensions, wettable powders, tablets, and micro-encapsulations) or in the tissue of the target crop which can be altered to express a *Bt* transgene (Lacey, Frutos, Kaya, and Vail 2001). The several strains of *B. thuringiensis* that are toxic to coleopteran larvae typically express *Cry3* toxins or the binary *Cry34/35* toxins (Bravo, Sarabia, Lopez, Ontiveros, and Quintero 1998; Baum et al. 2004; Bravo et al. 2005). Krieg, Huger, Langenbruch, and Schnetter (1983) were the first to report a *Bt* strain (var. *tenebrionis*) with activity against Coleoptera. Herrnstadt and Soares (1989) reported that spores and crystals of *Bt* (var. *tenebrionis*) are active against *Diabroticina*, including *D. v. virgifera* (Table 2). Subsequently, a strain of *Bt* (EG4961, var. *kurmamotoensis*) was shown to have moderate activity against larvae of *D. undecimpunctata howardi* (Rupar et al. 1991) via expression of a *Cry3B2* toxin (Donovan et al. 1992).

The binary-like toxins *Cry34/Cry35* were first discovered as a family of insecticidal proteins in a screen of *Bt* strains for activity against *D. v. virgifera* larvae (Ellis et al. 2002). In a follow-up survey, Schnepf et al. (2005) screened 6500 *Bt* isolates using DNA-hybridization probes for sequences related to *Cry35A* gene and identified 78 positive strains. Proteins that matched *Cry35* in mass (ca. 44 kDa) were observed in insecticidal protein preparations from 42 of these strains. Bioassays of these insecticidal protein preparations against neonate *D. v. virgifera* larvae indicated that strains producing *Cry35A* were only toxic if they also produced *Cry34B* (ca. 14 kDa). In this same study, recombinant acrySTALLIFEROUS *Bt* strains expressing *Cry34A/Cry35A* and *Cry34B/Cry35B* proteins were also tested for toxicity against neonate *D. v. virgifera* larvae; the *Cry34A/Cry35A* binary toxins were more active than the *Cry34B/Cry35B* toxins.

Transgenic maize hybrids expressing the *Cry3Bb1* gene (Vaughn et al. 2005) or *Cry34Ab1* and *Cry35Ab1* genes (Moellenbeck et al. 2001) are used extensively for *Diabrotica* control in North America (Ward et al. 2005). *Cry34Ab1* and *Cry35Ab1* transgenics received USA registration in 2005 and are much less susceptible to damage by *Diabroticina* larvae, including *D. v. virgifera*, *D. barberi* and *D. virgifera zea* (King, Neese, Edwards, and Thompson 2006). There are four foci in current research: (1) developing strategies against *Bt* resistance in *Diabrotica* (Onstad 2006;

Table 2. Records of bacteria, protista (= formerly protozoa) and virus species in the subtribe Diabroticina (Coleoptera: Chrysomelidae). Insecticidal proteins from *Bacillus thuringiensis* in transgenic crops not included. The taxonomy classification of the protista refers to Hausmann *et al.* (2003). Names of strains are presented in capital letters.

Host	Pathogen	Order: Family	Stage infected	Location	Reference
Bacteria					
<i>Acalymma blandulum</i> LeConte	<i>Wolbachia</i> sp.	Rickettsiales: Rickettsiaceae	adult	USA	Clark et al. 2001
<i>A. vittatum</i> (= <i>A. or D. vittata</i> ) (= <i>D. melanocephala</i> ) (F.)	<i>Wolbachia</i> sp.		adult	USA	Clark et al. 2001
<i>Cerotoma arcuata</i> (= <i>Andrector arcuatus</i> ) Olivier	<i>Bacillus thuringiensis</i> Berliner CG940	Bacillales: Bacillaceae	larva	Lab	Teixeira & Franco 2007
	<i>Serratia marcescens</i> Bizio***	Enterobacteriales: Enterobacteriaceae	adult***	Lab	Lord et al. 1987; Anonymous 2007
<i>Diabrotica balteata</i> LeConte	<i>Proteus mirabilis</i> Hauser	Enterobacteriales: Enterobacteriaceae	adult	USA	Schalk et al. 1987
	<i>Pseudomonas aeruginosa</i> Migula	Pseudomonadales: Pseudomonadaceae	adult	USA	Schalk et al. 1987
<i>D. barberi</i> Smith Lawrence	<i>Wolbachia</i> sp. (group A Type1 & 2)		adult	USA	Roehrdanz et al. 2002a,b; Roehrdanz & Levine 2007
<i>D. cristata</i> (Harris)	<i>Wolbachia</i> sp.		adult	USA	Clark et al. 2001
<i>D. lemniscata</i> LeConte	<i>Wolbachia</i> sp.		adult	USA	Clark et al. 2001
<i>D. undecimpunctata howardi</i> Barber	<i>B. thuringiensis</i> (var. <i>kurmamotoensis</i> ) EG4961		larva	Lab	Rupar et al. 1991
	<i>Chromobacterium subtsugae</i> Martin	Neisseriales: Neisseriaceae	adult	Lab	Martin et al. 2007
<i>D. v. virgifera</i> LeConte	<i>P. aeruginosa</i>		larva, adult	Lab	Hamilton 1968
	<i>B. thuringiensis</i> (var. <i>tenebrionis</i> ) SAN DIEGO		adult	Lab	Herrnstadt & Soares 1989
	<i>Ch. subtsugae</i>		adult	Lab	Martin et al. 2007
	<i>P. aeruginosa</i>		larva, adult	Lab	Hamilton 1968

Table 2 (Continued)

Host	Pathogen	Order: Family	Stage infected	Location	Reference
	<i>Wolbachia</i> sp. (group A)		adult, egg	Canada; USA	Giordano et al. 1997; Clark et al. 2001
<i>D. v. zae</i> Krysan & Smith	<i>Wolbachia</i> sp. (group A)		adult	Lab USA	Degrugillier et al. 1991 Giordano et al. 1997
<i>A. vittatum</i>	<i>Gregarina munieri</i> (Schneider)		–	–	Levine 1988
	<i>Gregarina</i> sp.		adult	USA	Brooks & Jackson 1990
	Protista				
<i>D. speciosa</i> (Germar)	<i>Gregarina</i> sp.	Eugregarinorida: Gregarinidae	adult	Brazil	Micheli 2005
<i>D. undecimpunctata howardi</i>	Unidentified Eugregarines	Eugregarinorida	adult	Lab	Jackson 1986
	<i>Gregarina coronata</i> Clopton, Percival Janovy		adult	USA	Clopton et al. 1992
<i>D. v. virgifera</i>	Unidentified Eugregarines		adult	Lab	Jackson 1986; Brooks & Jackson 1990
	Viruses				
<i>D. undecimpunctata</i> Mannerheim	Baculovirus-like particles		adult	USA	Kim & Kitajima 1984
<i>D. v. virgifera</i>	<i>Picorna</i> -like virus particles		adult	Lab	Degrugillier et al. 1991

\*\* denotes application of laboratory strains to the field

\*\*\* mainly considered as secondary or opportunistic pathogens (Lord et al. 1987)

Storer, Babcock, and Edwards 2006; Lefko et al. 2008; Nowatzki et al. 2008); (2) risk of non-target effects of transgenic maize (Al-Deeb, Wilde, Blair, and Todd 2003; O'Callaghan, Glare, Burgess, and Malone 2005); (3) discovery of new or modified toxins with greater virulence; and (4) developing plants which express toxins only in specific tissues and/or in response to pest infestation.

*Chromobacterium subtsugae* (Neisseriales: Neisseriaceae), a recently isolated gram-negative non-spore-forming forest-soil bacterium with violet pigment, was shown to be toxic to Colorado potato beetles (Martin, Blackburn, and Shropshire 2004). Addition of *C. subtsugae* to a watermelon juice mixture containing 0.05% cucurbitacin-E glycoside killed up to 100% of *Diabrotica* adults. Larvae fed freeze-dried artificial diet rehydrated with *C. subtsugae* suspension suffered only 40% mortality (Martin, Hirose, and Aldrich 2007). In this same study, bioassays with the green stink bug *Nezara viridula* L. (Heteroptera: Pentatomidae) suggested that mortality may be due to a heat-stable toxin produced and secreted into the growth medium by *C. subtsugae* (Martin et al. 2007). This observed toxicity is peculiar and unexpected from a bacterial group (Neisseriaceae) rarely associated with insects. Further investigation is necessary, and the potential incorporation of an adult-targeted (versus larva-targeted) agent in control strategies for *Diabrotica* pests in maize must be evaluated.

Many gram-negative bacteria are found in the intestinal tract of adult *D. balteata* and *D. undecimpunctata howardi* (Schalk, Peterson, and Hamalle 1987; Tran and Marrone 1988). Of the species identified, only *Pseudomonas aeruginosa* Migula (Pseudomonadales: Pseudomonadaceae) and *Proteus mirabilis* Hauser (Enterobacteriales: Enterobacteriaceae) are known insect pathogens. *Pseudomonas aeruginosa* was also isolated from laboratory cultures of *D. undecimpunctata* in South Dakota, USA, and has been shown to have potential in biological control against *D. undecimpunctata howardi* and *D. virgifera* (Hamilton 1968). However, it is a potential threat to human health.

Other potential bacterial agents, frequently found associated with chrysomelid beetles, have yet to be found in Diabroticina. A number of maize-associated rhizosphere bacteria, such as *Serratia* spp. (Proteobacteria: Enterobacteriaceae) have recently been identified; these may influence the interactions of *Diabrotica* spp. larvae with the crop (Prischmann, Lehman, Christie, and Dashiell 2008). Moreover, *Serratia marcescens* (BN10) Bizio was isolated from the alder leaf beetle, *Agelastica alni* L. (Coleoptera: Chrysomelidae) (Sezen, Demir, and Demirbag 2004), while products of congener *S. entomophila* Grimont are used to control the grass grub *Costelytra zealandica* (White) (Coleoptera: Scarabaeidae) in turf grass (O'Callaghan and Jackson 1993; O'Callaghan and Gerard 2005; Tan, Jackson, and Hurst 2006).

*Wolbachia* (Rickettsiaceae) are obligate intracellular bacteria that infect arthropods, including many economically important insects, and in some cases profoundly affect host reproduction (Floate, Kyei-Poku, and Coghlin 2006). The most common phenotype caused by *Wolbachia* infection is cytoplasmic incompatibility, which results in embryonic mortality from mating between partners with differing *Wolbachia* infection status (Floate et al. 2006). The Rickettsia-like-bacteria detected by Degrugillier et al. (1991) in the cytoplasm of spermatocyst cells of the testes of *D. v. virgifera* in an ultra-structural study are now thought to be *Wolbachia*, providing the first evidence for association of *Wolbachia* with *Diabrotica* species. Subsequently, natural populations of several *Diabrotica* spp. were screened with

*Wolbachia*-specific PCR primers targeting 16SrRNA and *ftsZ* gene sequences, detecting *Wolbachia* infections in *D. v. virgifera* and *D. virgifera zea* from the USA and Canada (Giordano, Jackson, and Robertson 1997). Clark, Meinke, Skoda, and Foster (2001) also detected *Wolbachia* in two other *Diabrotica* species and two *Acalymma* species in the USA (Table 2). Using beetles treated with tetracycline to obtain *Wolbachia* free colonies, Giordano et al. (1997) demonstrated that *Wolbachia* causes unidirectional cytoplasmic incompatibility between *D. v. virgifera* and *D. v. zea*. Conversely, when *Wolbachia*-infected *D. v. virgifera* males were mated with tetracycline-treated females only 0.4% of 5627 eggs hatched, although untreated females of the same population were compatible. According to DNA phylogeny, the *Wolbachia* in *Diabrotica* spp. belong to group-A-*Wolbachia* (Giordano et al. 1997; Clark et al. 2001; Roehrdanz, Levine, and Degrugillier 2002a,b; Roehrdanz and Levine 2007). The potential for using *Wolbachia* species in biological control strategies is discussed by Zabalou et al. (2004) and Floate et al. (2006), but has not been applied to control Diabroticina or any other insect to date.

### Protista

Protist (=formerly protozoan) diseases of insects, e.g. flagellates, eugregarines and schizogregarines (McLaughlin et al. 2001; Hausmann, Hülsmann, and Radek 2003) are omnipresent and play an important role in regulating insect populations (Brooks 1988). Most protista are host-specific and cause chronic infections that affect reproduction and overall fitness (Lacey et al. 2001). Eugregarine protista have been found in field-collected and laboratory-reared Diabroticina beetles, respectively (Table 2) (Levine 1988; Brooks and Jackson 1990; Clopton 1992; Micheli 2005). The protista in Diabroticina are typically commensal and facultative pathogens that increase adult mortality and inhibit ovarian and fat body development. Micheli (2005) reported season-dependent infection levels of adult *D. speciosa* with *Gregarina* sp. (Eugregarinorida: Gregarinidae) in field populations in Brazil, i.e. being high from February to August (maximum 96.7%), and below 10% from September to January. However, the impact of protista on Diabroticina pest populations in the field is mostly unknown and needs further investigation (Levine and Oloumi-Sadeghi 1991).

### Viruses

Among viruses, members of the Baculoviridae (*Nucleopolyhedrovirus* and *Granulovirus*) offer the greatest potential for development as microbial-based insecticides (Miller, O'Reilly, and Dall 1999) and many are registered and used for inundative biological control of lepidopterans, including the *Helicoverpa zea* nucleopolyhedrovirus for control of *Heliothis* and *Helicoverpa* spp. (Copping 2004). Some viruses have been successfully used in augmentation approaches, including the *Oryctes* virus for control of the coconut palm rhinoceros beetle, *Oryctes rhinoceros* (Coleoptera: Scarabaeidae) (Huger 2005).

Potential viral biological control agents are nearly unexplored in Diabroticina. Only two viruses have been described (Table 2) from Diabroticina beetles: (1) Kim and Kitajima (1984) found putative non-occluded baculovirus-like particles in haemocytes and midgut cells of *D. undecimpunctata*, but without any apparent



negative effects on the beetles. Moreover, the identification of this virus may need to be revised (Herniou, Olszewski, Cory, and O Reilly 2003; Theilmann et al. 2005; Jehle 2006). (2) Large masses of *Picornia*-like virus particles (24–26 nm) were found in the cytoplasm of spermatocyst cells of adult *D. v. virgifera*, during an ultra-structural study by Degrugillier et al. (1991), but proper taxonomic identification of the virus and bioassays for virulence are still lacking.

### Macrobials

The fauna of nematodes and arthropods attacking *Diabroticina* is more diverse than previously assumed (Eben and Barbercheck 1996; Lundgren, Nichols, Prischmann, and Ellsbury, in press) and warrants more attention. Nematodes are gaining popularity in pest control, and species that are already commercially available may prove useful for inundative biological control of *Diabroticina*.

Recently, the use of species-specific molecular markers is providing insights into the range and impact of predators on *Diabroticina*, suggesting possibilities for control through conservation of natural enemies (J. Lundgren, personal communication).

There are no parasitoids known of eggs or larvae of any *Diabroticina* species; and less than 10 species in two genera of parasitoids seem to parasitize adult *Diabroticina*. Most of those species are relatively host-specific, and may be useful for classical biological control of invasive *Diabroticina*, i.e. *D. v. virgifera* in Europe and North America (Toepfer et al. 2008b).

### Nematodes

Entomopathogenic nematodes have been successfully used as biological control agents against a wide range of different insect pests (Grewal, Ehlers, and Shapiro 2006); some of them show potential in controlling *Diabrotica* larvae in field crops (Jackson and Brooks 1989; Jackson 1996; Toepfer, Gueldenzoph, Ehlers, and Kuhlmann 2005) (Table 3). Nine genera in six families of nematodes are known to naturally attack *Diabroticina* in the field: *Heterorhabditis* Poinar (Rhabditida: Heterorhabditidae), *Steinernema* Travassos (Rhabditida: Steinernematidae), *Panagrolaimus* Fuchs (Rhabditida: Panagrolaimidae), *Howardula* Cobb. (Tylenchida: Allantonematidae), *Agamermis* Cobb., *Hexamermis* (Steiner), *Oesophagomermis* (= *Filipjevimermis*) Artyukhovsky (all Mermithida: Mermithidae), *Micoletzkyia* Weingartner and *Diplogaster* Schultze (both Diplogasterida: Diplogasteridae) (Table 3).

Steinernematidae and Heterorhabditidae are commercially available and the best-studied of these families (Kuhlmann and van der Burgt 1998; Cabanillas, Wright, and Vyas 2005); but natural host records in *Diabroticina* are limited. *Heterorhabditis* species were recorded from larvae of *D. balteata* in South Carolina, USA (Creighton and Fassuliotis 1985), *D. u. howardi* in North Carolina, USA (Brust 1991c) and *D. v. virgifera* in Hungary (Pilz et al. 2008) (Table 3). *Steinernema* species were recorded from larvae of *D. u. howardi* in Virginia, USA (Fronck 1950) and *D. v. virgifera* in Hungary (Pilz et al. 2008). No records of Steinernematidae or Heterorhabditidae exist from other genera of *Diabroticina* such as *Acalymma* or *Cerotoma*. Field records of *Heterorhabditis* and *Steinernema* from any adult *Diabroticina* do not exist either, although the beetles could be vulnerable while emerging or laying eggs into

Table 3. Records of entomopathogenic nematodes attacking species in the subtribe Diabroticina (Coleoptera: Chrysomelidae). Names of strains are presented in capital letters.

Host	Nematode	Order: Family	Stage attacked	Location	Reference
<i>Acalymma vittatum</i> (= <i>A. or D. vittata</i> ) (= <i>D. Melanocephala</i> ) (F.)	<i>Heterorhabditis bacteriophora</i> (Poinar)	Rhabditida: Heterorhabditidae	larva	Lab	Reed et al. 1986
	<i>Howardula benigna</i> Cobb	Tylenchida: Allantonematidae	adult	USA	Cobb 1921a,b; Elsey 1977; Fischer 1981
	<i>Steinernema riobrave</i> Cabanillas, P.R.**	Rhabditida: Steinernematidae	larva	USA**	Ellers-Kirk et al. 2000**
	<i>Steinernema</i> (= <i>Neoplectana</i> ) <i>carpocapsae</i> (Weiser)		larva	Lab	Reed et al. 1986
<i>A. fairmairei</i> (F.)	<i>Agamermis</i> sp.	Mermithida: Mermithidae	adult	Mexico	Eben & Barbercheck 1996
	<i>Hexamermis</i> sp.	Mermithida: Mermithidae	adult	Mexico	Eben & Barbercheck 1996
<i>A. trivittatum</i> (= <i>trivittata</i> ) (Mannerheim)	<i>H. benigna</i>		adult	USA	Cobb, 1921a,b
<i>C. trifurcata</i> (Forster)	<i>Diplogaster</i> sp.	Diplogasterida: Diplogasteridae	overwintering adult	USA	Payah & Boethel 1986
<i>Diabrotica amecameca</i> Kryan Smith	<i>Hexamermis amecamecae</i> nov. sp. (Stock)		adult	Mexico	P. Stock & A. Eben 2000, 2004, unpubl. data
<i>D. balteata</i> LeConte	<i>Oesophagomermis</i> (= <i>Filipjevimermis</i> ) <i>leipsandra</i> (Poinar and Welch)	Mermithida:	larva	USA	Cuthbert 1968; Poinar 1968
		Mermithidae			
				Lab, USA**	Creighton & Fassuliotis 1980, 1981, 1982, 1983**; Elsey 1989**
	<i>Heterorhabditis</i> sp.		larva	USA	Creighton & Fassuliotis 1985
	<i>Hexamermis</i> sp.		adult	Mexico	Eben & Barbercheck 1996
	<i>S. carpocapsae</i>		larva	Lab	Schalk et al. 1993

Table 3 (Continued)

Host	Nematode	Order: Family	Stage attacked	Location	Reference
	<i>S. carpocapsae</i> DD-136, RAEA57820**		larva	Lab, USA**	Creighton et al. 1968**
<i>D. barberi</i> Smith Lawrence	<i>Steinernema feltiae</i> (Filipjev) (= <i>S. or Neoplectana bibionis</i> )**		larva	Lab, Canada**	Thurston & Yule 1990**
<i>D. porracea</i> Harold	<i>Hexamermis</i> sp.		adult	Mexico	Eben & Barbercheck 1996
<i>D. speciosa</i> (Germar)	<i>Hexamermis</i> sp.		adult	Peru	Nickle et al. 1984
				Brazil	Heineck-Leonel & Salles 1997
	<i>Micoletzkyia vidalae</i> (Stock)****	Diplogasterida: Diplogasteridae	larva	Argentina	Stock 1993
<i>D. tibialis</i> Baly	<i>Hexamermis</i> sp.		adult	Mexico	Eben & Barbercheck 1996
<i>D. undecimpunctata howardi</i> Barber	<i>Diplogaster</i> sp.****		adult	Argentina	G. Cabrera Walsh, 2004, unpubl. data
	<i>O. leipsandra</i> **		larva	Lab, USA**	Cuthbert, 1968
	<i>H. bacteriophora</i>		larva	Lab	Barbercheck 1993; Ellers-Kirk 2000
	<i>H. bacteriophora</i> LEWISTON		larva	Lab	Eben & Barbercheck 1997
	<i>Heterorhabditis heliothidis</i> (= <i>H. bacteriophora</i> )		larva	USA	Brust 1991c
	<i>Hexamermis</i> sp.		adult	Lab	Nickle et al. 1984
	<i>H. benigna</i>		adult	USA	Cobb 1921a,b; Fronck 1950; Elsey 1977
	<i>Steinernema</i> sp. (= <i>Neoplectana</i> sp.)		adult	USA	Fronck 1950
	<i>S. carpocapsae</i>		larva	Lab	Barbercheck 1993, 2003; Ellers-Kirk 2000
	<i>S. carpocapsae</i> AGRIOTOS, MEXICAN		larva	Lab	Eben & Barbercheck 1997

Table 3 (Continued)

Host	Nematode	Order: Family	Stage attacked	Location	Reference
<i>D. u. undecimpunctata</i> Mannerheim	<i>S. feltiae</i>		larva	Lab	Ellers-Kirk 2000
	<i>S. riobrave</i>		larva	Lab	Ellers-Kirk 2000
	<i>O. leipsandra</i>		larva	USA	Poinar 1968a
	<i>H. bacteriophora</i> NC1		larva	Lab	Choo et al. 1996
	<i>S. carpocapsae</i> US ALL		larva	Lab	Choo et al. 1996
	<i>S. riobrave</i> TEXAS		larva	Lab	Choo et al. 1996
	<i>H. bacteriophora</i>		larva	Lab	Kaya et al. 1995
<i>D. undecimpunctata</i> (= <i>12-punctata</i> ) Mannerheim	<i>S. carpocapsae</i>		larva	Lab	Kaya et al. 1995
	Unidentified Mermithidae species	Mermithida: Mermithidae	adult	USA	Rockwood & Chamberlain 1943
<i>D. v. virgifera</i> LeConte	<i>H. bacteriophora</i> LEWISTON		larva	Lab	Georgis et al. 1991; Jackson 1996
	<i>H. bacteriophora</i> EUR US HYBRID**		larva	Hungary**	Toepfer et al. 2008a**
	<i>H. bacteriophora</i> EUR US HYBRID		larva, pupa	Lab	Toepfer et al. 2005, Kurtz <i>et al.</i> 2008
	<i>H. bacteriophora</i>		larva,	Lab	Jackson & Hesler 1996
	<i>H. bacteriophora</i> HU-2, HU-1, HU-MOL		adult	Lab	van der Burgt et al. 1998
	<i>H. bacteriophora</i> KOH HBMVHELY HUNGARY, HU10, HU15		adult	Lab	Zijlstra 1998
	<i>Heterorhabditis megidis</i> (Poinar, Jackson, Klein) SWISS NL-H-W79		larva, pupa	Lab	Rasmann et al. 2005; Kurtz et al. 2008
	<i>H. megidis</i> SWISS NL-H-W79**		larva	Hungary**	Rasmann et al. 2005** ; Toepfer et al. 2008 a**
	<i>Heterorhabditis</i> sp.		larva	Hungary	Pilz et al. 2008
	<i>Micoletzkyia</i> sp.****		larva	Hungary	Toepfer et al. 2004

Table 3 (Continued)

Host	Nematode	Order: Family	Stage attacked	Location	Reference
	<i>Panagrolaimus</i> sp.****	Rhabditida: Panagrolaimidae	larva	Hungary	Toepfer et al. 2004
	<i>Steinernema abassi</i> (Elawad, Ahmad, Reid) PALESTINE		larva	Lab	Toepfer et al. 2005
	<i>Steinernema arenarium</i> (= <i>anomali</i> ) (Artyukhovsky)		adult	Lab	van der Burgt et al. 1998
	<i>S. arenarium</i> (Artyukoovsky) POLAND		larva	Lab	Toepfer et al. 2005
	<i>S. carpocapsae</i>		larva	Lab	Munson et al. 1970; Toepfer et al. 2005
	<i>S. carpocapsae</i> **		larva	USA**	Journey & Ostlie 2000**;
					Nishimatsu & Jackson 1998**
	<i>S.</i> (= <i>Neoplectana</i> ) <i>carpocapsae</i> US ALL, AGRIOTOS, MEXICAN, BECTON, DD-136, BRETON**		larva	USA**	(Peters 1986a,b; Jackson & Hesler 1996; Nickle et al. 1994; Wright et al. 1993; Schalk et al. 1993; Georgis et al. 1991)**
	<i>S.</i> (= <i>Neoplectana</i> ) <i>carpocapsae</i> (here <i>feltiae</i> ***)		larva	Lab	(Gaugler 1981; Jackson & Brooks 1989; 1995; Poinar et al. 1982; Poinar et al. 1983)***
	(Filipjev) USA ALL, AGRIOTOS, MEXICAN				
	<i>S.</i> (= <i>Neoplectana</i> ) <i>carpocapsae</i> (here <i>feltiae</i> ***)**		larva	USA**	(Thurston and Yule 1990**;
	<i>S. feltiae</i> **		larva	USA**	Poinar et al. 1983**)*
	<i>S. feltiae</i> FA-1, ISRAEL		adult	Lab	Riga et al. 2001**
	<i>S. feltiae</i> EUR US HYBRID		larva, pupa	Lab	van der Burgt et al. 1998
					Toepfer et al. 2005; Kurtz et al. 2008
	<i>S. feltiae</i> EUR US HYBRID		larva	Hungary**	Toepfer et al. 2008a**

Table 3 (*Continued*)

Host	Nematode	Order: Family	Stage attacked	Location	Reference
	<i>S. glaseri</i> (Steiner)**		larva	USA**	Riga 2001**
	<i>S. glaseri</i> NC		larva	Lab	Toepfer et al. 2005
	<i>S. bicornutum</i> (Tallosi, Peters, Ehlers) SERBIA		larva	Lab	Toepfer et al. 2005
	<i>S. kraussei</i> (Steiner) BELLIN		larva	Lab	Toepfer et al. 2005
	<i>Steinernema</i> sp.		larva	Hungary	Pilz et al. 2008
<i>Diabrotica</i> sp.	<i>H. benigna</i> .		larva		Cobb 1921a,b; Fronk 1950

\*\* denotes application of laboratory strains to the field

\*\*\* studies on *S. feltiae* before 1990, as well as Jackson and Brooks 1995, were synonymous to *S. carpocapsae*, as the taxonomy of *S. feltiae* was still not clarified at that time (A. Peters, J. Jackson, 2006, pers. comm.)

\*\*\*\* insect-associated but not entomopathogenic nematodes (Toepfer and Kuhlmann 2004)

the soil, and *D. v. virgifera* adults have been successfully attacked in the laboratory by *S. feltiae* (Filipjev), *S. arenarium* (= *S. anomali*) (Artyukhovsky), and *H. bacteriophora* (Poinar) (Table 3) (van der Burgt, Budai, Lucskai, and Fodor 1998).

The success of control of *Diabroticina* larvae with different species and strains of *Steinernema* and *Heterorhabditis* is highly variable (Peters 1986a,b; Kuhlmann and van der Burgt 1998; Cabanillas et al., 2005). Laboratory tests, particularly on *Diabrotica* species, show that nematodes can inflict high levels of larval mortality, but field results vary greatly with environmental conditions, including: soil moisture and application techniques (Munson and Helms 1970; Georgis, Kaya, and Gaugler 1991; Barbercheck 1993; Jackson and Brooks, 1996), the source and host-specificity of the nematode strains (Jackson and Brooks 1996), and on their host-finding strategy (Rasman et al. 2005), survival, movement and persistence in the soil (Georgis et al. 1991; Barbercheck 1993; Jackson and Brooks 1996).

Mass-produced for biological control since the 1980s, *Steinernema carpocapsae* (= *Neoplectana carpocapsae*) (Weisser) has been intensively studied for controlling larvae of *Diabrotica* species (Jackson and Brooks 1996). *Steinernema carpocapsae* was also synonymous to *S. feltiae* in papers published from 1980 to about 1995 (A. Peters and J. Jackson, personal communication, 2006), such that some references cited here, Munson and Helms (1970); Gaugler (1981); Poinar et al. (1982); Jackson and Brooks (1989, 1996) actually dealt with *S. carpocapsae* and not the named *S. feltiae* (see details in Table 3). Only one strain of *S. carpocapsae*, i.e. MEXICAN STRAIN, has been shown effective against *D. v. virgifera* larvae in the laboratory, exhibiting a 20-times higher efficacy than the other strains tested (e.g. US ALL, AGRIOTOS, DD-136) (Munson and Helms 1970; Jackson and Brooks 1989, 1996; Toepfer et al. 2005). In greenhouse or laboratory experiments, *S. carpocapsae* caused more than 90% larval mortality of *D. balteata*, *D. undecimpunctata howardi* (Schalk, Bohac, Dukes, and Martin 1993) and *D. v. virgifera* (Nickle, Schroder, and Krysan 1984). In field experiments, Wright, Witkowski, Echtenkamp, and Georgis (1993) and Journey and Ostlie (2000) successfully used high concentrations of *S. carpocapsae* against *D. v. virgifera* and *D. barberi*. Jackson and Brooks (1996) suggested that application of *S. carpocapsae* is most effective when second and third instar *Diabrotica* are predominant in the field. *Steinernema carpocapsae* ambushes its prey (Gaugler 2002), and thus may be less likely than more active non-ambushing nematode species, e.g. *S. glaseri* (Steiner), *H. megidis* (Poinar, Jackson, Klein), or *H. bacteriophora*, to migrate towards *Diabrotica*-infested roots.

*Steinernema feltiae* (Filipjev), formerly described as *S. bibionis* (= *Neoplectana bibionis*), is known to be a generalist with only moderate efficacy against specific insect targets (Peters 1996). *Steinernema feltiae* was highly virulent against *D. v. virgifera* larvae in laboratory trials (Toepfer et al. 2005), but its propagation was relatively low (about 2200 juveniles per third instar beetle larva). Applications of *S. feltiae* during maize seeding reduced the number of first instar *D. barberi* larvae in Quebec, Canada (Thurston and Yule 1990) and all instars of *D. v. virgifera* in Hungary (Toepfer, Peters, Ehlers, and Kuhlmann 2008a).

Strains of *S. glaseri*, *S. arenarium* and *S. kraussei* (Steiner) (Table 3) were found to be highly virulent against *D. v. virgifera* larvae under laboratory conditions, whereas *S. abassi* (Elawad, Ahmad, Reid) and *S. bicornutum* (Tallosi, Peters, Ehlers) were less effective (Toepfer et al. 2005). Riga, Wistlecrafft, and Potter (2001) reported successful control of *D. v. virgifera* larvae with *S. glaseri* in greenhouse experiments in

Canada. However, large-scale applications of *S. glaseri* or *S. arenarium* may be impractical because neither species is easily mass-produced in liquid culture (Ehlers 2001).

*Heterorhabditis megidis* (NL-H-W79) controlled up to 70% of *D. v. virgifera* larvae and pupae in both laboratory and field trials (Rasmann et al. 2005; Kurtz, Toepfer, Ehlers, and Kuhlmann 2008; Toepfer et al. 2008a). Nematodes of this species are attracted by the plant-root volatile  $\beta$ -caryophyllene produced upon *D. v. virgifera* larval attack (Rasmann et al. 2005). *Heterorhabditis megidis* may be an excellent biological control agent for caryophyllene-emitting maize hybrids.

Laboratory tests showed *H. bacteriophora* to be effective against *D. v. virgifera* (up to 90% mortality) (Jackson 1996; Toepfer et al. 2005). A mean of about 4000 juvenile nematodes propagated from each infected third instar *D. v. virgifera* (Toepfer et al. 2005). Georgis et al. (1991) and Toepfer et al. (2008a) demonstrated that *H. bacteriophora* can also significantly reduce *D. v. virgifera* under field conditions without affecting the abundance of most other soil arthropods. Furthermore, a combined application of *S. carpocapsae*, *H. bacteriophora* and pesticide soap (M-Pede, Dow AgroSciences) was more effective against larvae of *D. u. undecimpunctata* in greenhouse tests than a treatment of either nematode alone (Kaya, Burlando, Choo, and Thurston 1995).

In general, entomopathogenic nematodes are strongly influenced by cultural practices in crops. *Heterorhabditis bacteriophora*, *H. megidis* and *S. feltiae* persisted for only about 3 months in conventionally tilled maize fields in Hungary, and were not detected in the following year (Kurtz, Toepfer, Ehlers, and Kuhlmann 2007). In contrast, the infection of *Diabrotica* by *S. carpocapsae* was still occurring 3 years after application (J. Jackson, personal communication, 2006) with a centre pivot in a North American maize field (Ellsbury, Jackson, Woodson, Beck, and Strange 1996b). By varying three cultural methods – tillage, weed control and soil irrigation – Brust (1991c) was best able to foster densities of the endemic nematode *H. heliothidis* (= *H. bacteriophora*) for effective control of artificial infestations of *D. undecimpunctata howardi* with low tillage systems and less intensive weed control.

Because of their short life cycle and favourable mass-rearing techniques, nematodes can be selected for traits that increase their efficacy. For example, T. Turlings and M. Baroni (personal communication, 2007) successfully selected *H. bacteriophora* for better recognition of  $\beta$ -caryophyllene and found higher control efficacies against *D. v. virgifera* than by the unselected strain. In contrast, after rearing nematodes on a single target host, *D. undecimpunctata howardi*, Barbercheck, Wang, and Brownie (2003) did not observe an increase in infectivity on the target host. This was unexpected since other studies have shown selection and adaptation in nematode-insect associations (Gerritsen, Weigers, and Smith 1998). Barbercheck et al. (2003) were, however, successful in selecting nematodes with superior ability to locate *Diabrotica*-damaged plants.

Mermithids, such as *Hexameris* spp. were found in adult *D. speciosa* in Argentina (Cabrera Walsh 2003) and Peru (Nickle et al. 1984), where 5–90% infection rates were observed. Field and laboratory tests in Maryland, USA indicate that *Hexameris* spp. attack a broad range of beetle hosts, including: *D. undecimpunctata howardi*, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), and *Epilachna varivestis* Mulsant (Coleoptera; Coccinellidae) (Nickle et al. 1984). In Mexico, an undescribed *Hexameris amecamecae* nov. sp. Stock was



found in adults of *D. amecameca* Krysan and Smith, and a second undescribed *Hexameris* sp. was found in *D. balteata*, *D. porracea*, *D. tibialis*, and *Acalymma fairmairei* (F.) (Eben and Barbercheck 1996; P. Stock and A. Eben, personal communication, 2004). An *Agameris* sp. was found on *Acalymma fairmairei* in Mexico (A. Eben, personal communication, 2000). *Oesophagomermis* (= *Filipjevimermis*) *leipsandra* Poinar and Welch was found on larvae of *D. balteata* in South Carolina, USA (Cuthbert 1968). Laboratory, greenhouse and field studies were carried out to evaluate the effectiveness of this mermithid in controlling larvae of *D. balteata* and *D. u. howardi* on maize (Creighton and Fassuliotis 1983). In cage tests in field plots, an application of *O. leipsandra* eggs to the soil resulted in a parasitism rate of 50–100% (Creighton and Fassuliotis 1983). The biology, potential host range, and possible rearing methods of *O. leipsandra* are described by Cuthbert (1968) and Creighton and Fassuliotis (1980, 1981, 1982). Since mermithid nematodes are obligate parasites and difficult to mass rear *in vivo*, they are currently not being considered for biological control (A. Peters, personal communication, 2006).

*Howardula benigna* Cobb (Tylenchida: Allantonematidae) was frequently found in adults of *D. undecimpunctata howardi* Barber (Fronk 1950; Elsey 1977) (Table 3). Another allantonematid, the facultative parasite *Micoletzkyia vidalae* Stock, was occasionally found in *D. speciosa* larvae in Argentina (Stock 1993) and an unidentified *Micoletzkyia* sp. was found in *D. v. virgifera* larvae in Hungary (Toepfer and Kuhlmann 2004). Records of less common nematode genera or families found in Diabroticina are listed in Table 3.

### Arthropod predators

Generalist predators are abundant and diverse within agro-ecosystems, and consume a wide array of insect pests (e.g. Chang and Kareiva 1999; Symondson, Sunderland, and Greenstone 2002; Lundgren, Shaw, Zaborski, and Eastman 2006). Known predators of Diabroticina occur in 35 families from 12 different orders (Table 4), but most records are somewhat superficial; the associations reported are simple, between single-species (i.e. a designated predator with the target beetle), and are often based on laboratory no-choice experiments. Three groups of Diabroticina predators have been most studied: mites (Acari), ants (Formicidae), and carabid beetles (Carabidae) (Table 4). However, comprehensive descriptions of the relative impacts of predator communities on Diabroticina within a region are rare. One such study examining the predator community in USA maize fields found that 17 taxa of predators consume *D. v. virgifera* eggs and larvae (based on analysis of gut contents using diagnostic molecular markers for *D. v. virgifera*, J. Lundgren, unpublished data). Of these, phalangids (Phalangida) and staphylinids (<5 mm in length) were the most abundant rootworm predators, but two carabids and two lycosids (Araneae) relied most frequently on *D. v. virgifera* immatures as prey. In an earlier study on the predator community associated with *D. undecimpunctata howardi*, many arthropods were observed to feed on eggs of the pest in the field, including: mesostigmatid mites e.g. *Tyrophagus putrescentiae* (Acaridae); larvae of cantharids, carabids and staphylinids; carabid adults, centipedes, and ants (Brust 1990).

Predaceous mites are abundant in agro-ecosystems (Welbourne 1982; Santiago-Blay and Fain 1994). These predators, although polyphagous, have been shown to be important in reducing the densities of *Diabrotica* immatures under field conditions

Table 4. Records of arthropod predators that prey on species in the subtribe Diabroticina (Coleoptera: Chrysomelidae).

Host	Predator	Order: Family	Stage attacked	Location	Reference
<i>Acalymma blomorum</i> Munroe Smith	<i>Oxyopes salticus</i> Hentz	Araneae: Oxyopidae	adult	Mexico	Eben & Barbercheck 1996
	<i>Repipta flavicans</i> Stal	Hemiptera: Reduviidae	adult	Mexico	Eben & Barbercheck 1996; Gamez-Virues & Eben 2005
<i>A. vittatum</i> (F.) (= <i>A. or D. vittata</i> ) (= <i>D. melanocephala</i> )	<i>Sinea diadema</i> F.	Hemiptera: Reduviidae	adult	USA	Chittenden 1919
	<i>Nabis ferus</i> L.	Hemiptera: Nabidae	adult	USA	Chittenden 1919
	<i>Phymata pennsylvanica</i> Handlirsch	Hemiptera: Phymatidae	adult	USA	Balduf 1939
	<i>Uropoda</i> sp.	Mesostigmata: Uropididae	Unknown	South America	Thompson & Simmonds 1965
	<i>Trombidium</i> sp.	Actinedida: Trombidiidae	Unknown	USA	Welbourne 1982
	<i>Cerotoma trifurcata</i> (Foerster)		adult	USA	Peterson et al. 1992; Danielson et al. 2000
<i>Diabrotica balteata</i> LeConte	<i>Trombidium hyperi</i> Vercammen-Grandjean		adult	USA	Peterson et al. 1992
	<i>O. salticus</i>		adult	Mexico	Eben & Barbercheck 1996
	<i>Caloglyphus</i> sp. Berlese	Astigmata: Acaridae	pupa	Lab	Saba 1970
	<i>Labidura riparia</i> Pallas	Dermaptera: Labiduridae	adult	Lab	Waddill 1978
	—	Hemiptera: Reduviidae	adult	Mexico	Eben and Barbercheck 1996
	<i>Proctolaelaps hypudaei</i> (Oudmans)	Mesostigmata: Ascidae	larva, pupa, adult	Lab	Saba 1970
<i>D. duodecimpunctata</i>	<i>Ph. pennsylvanica</i>		adult	USA	Badulf 1939

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
<i>D. longicornis</i> (Say)	<i>Carabus nemoralis</i> O.F. Müller	Coleoptera: Carabidae	egg	Lab	Tyler & Ellis 1979
	<i>Clivina fossor</i> L.	Coleoptera: Carabidae	egg, larva	Lab	Tyler & Ellis 1979
	<i>Pterostichus melanarius</i> (Illiger)	Coleoptera: Carabidae	egg, larva	Lab	Tyler & Ellis 1979
	<i>Bembidion quadrimaculatum oppositum</i> Say	Coleoptera: Carabidae	larva	Lab	Tyler & Ellis 1979
	<i>Harpalus pennsylvanicus</i> (De Geer)	Coleoptera: Carabidae	larva	Lab; Canada	Tyler & Ellis 1979; Kirk 1973a,b
	<i>Tachys</i> sp.	Coleoptera: Carabidae	larva	Lab	Tyler & Ellis 1979
	<i>Trechus apicalis</i> Motschulsky	Coleoptera: Carabidae	larva	Lab	Tyler & Ellis 1979
	<i>Phymata erosa</i> (L.)		adult	Canada	Dominique & Yule 1984
	<i>Ph. pennsylvanica</i>		adult	USA	Balduf 1939
	<i>Androlaelaps</i> sp.	Mesostigmata: Laelapidae	egg, larva	USA	Mihm & Chiang 1976
	<i>Stratiolaelaps</i> sp.	Mesostigmata: Laelapidae	egg, larva	USA	Chiang 1970, Mihm & Chiang 1976
<i>D. speciosa</i> (Germar)	–	Araneae	adult	Brazil	Bercellini & Malacalza 1994
	<i>Lebia concinna</i> Brullé	Coleoptera: Carabidae	adult	Brazil	Milanez 1984; Bercellini & Malacalza 1994; Hohmann 1989
	<i>Cycloneda sanguinea</i> (L.)	Coleoptera: Coccinellidae	–	Brazil	Hohmann 1989
	<i>Eriopis</i> sp.	Coleoptera: Coccinellidae	adult	Brazil	Bercellini and Malacalza 1994
	<i>Scymnus</i> spp.	Coleoptera: Coccinellidae	adult	Brazil	Hohmann 1989

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
<i>D. undecimpunctata</i> Mannerheim <i>D. undecimpunctata howardi</i> Barber	<i>Doru lineare</i> (Eschscholtz)	Dermaptera: Forficulidae	adult	Brazil	Milanez 1984
	<i>Orius</i> sp.	Hemiptera: Anthocoridae	adult	Brazil	Bercellini & Malacalza 1994; Hohmann 1989
	<i>Nabis</i> sp.		adult	Brazil	Milanez 1984; Bercellini & Malacalza 1994
	—	Hymenoptera: Vespidae	adult	Brazil	Picano et al. 1998
	<i>Chrysopa</i> sp.	Neuropetera: Chrysopidae	adult	Brazil	Bercellini & Malacalza 1994
	<i>Ph. pennsylvanica</i>		adult	USA	Balduf 1939
	<i>Tyrophagus putrescentiae</i> Schränk	Astigmata: Acaridae	larva	USA	Brust & House 1990; Brust 1990
	<i>Hogna helluo</i> and other Lycosidae	Araneae: Lycosidae	adult	Lab	Snyder & Wise 2000; Williams et al. 2001
	<i>Phidippus audax</i> (Hentz)	Araneae: Salticidae	adult	USA	Young 1989
	<i>Misumena vatia</i> (Clerck)	Araneae: Thomisidae	adult	USA	Lockley et al. 1989
	—	Chilopoda	larva	USA	Brust 1991b; Brust & House 1990
	—	Coleoptera: Cantharidae	larva	USA	Brust 1991b; Brust & House 1990
	<i>Anisodactylus</i> sp.	Coleoptera: Carabidae	larva	USA	Fronck 1950
	<i>Agonum</i> sp.	Coleoptera: Carabidae	larva	USA	Fronck 1950
	<i>Amara</i> sp.	Coleoptera: Carabidae	larva	USA	Fronck 1950

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
	<i>Pterostichus</i> sp.		larva	USA	Fronck 1950
	<i>Xantholinus</i> sp.	Coleoptera: Staphylinidae	larva	USA	Fronck 1950
	<i>Apiomerus crassipes crassipes</i> (F.)	Hemiptera: Reduviidae	adult	Lab	Morrill 1975
	<i>Lasius</i> spp.	Hymenoptera: Formicidae	egg, larva	USA	Brust 1991b
	<i>Solenopsis saevissima richteri</i> Forel	Hymenoptera: Formicidae	adults	Lab	Hays & Hays 1959
<i>D. u. undecimpunctata</i> Mannerheim	<i>Ph. audax</i>		adult	USA	Johnson 1996
<i>D. virgifera</i> LeConte	<i>Androlaelaps</i> sp.		egg, larva	USA	Chiang 1970
	<i>Myrmica americana</i> Weber	Hymenoptera: Formicidae	egg	Lab	Ballard & Mayo 1979
	<i>Pheidole bicarinata longula</i> Emery	Hymenoptera: Formicidae	egg	Lab	Ballard & Mayo 1979
<i>D. virgifera virgifera</i> LeConte	<i>Agelena</i> sp.	Araneae: Agelinidae	adult	Hungary	Tóth et al. 2002
	<i>Argiope bruennichi</i> (Scopoli)	Araneae: Araneidae	adult	Romania	I. Grozea 2008, pers. comm.
	<i>Lepthyphantes</i> sp.	Araneae: Linyphiidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Oedothorax apicatus</i> (Blackwall)	Araneae: Linyphiidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	—	Araneae:	larva	USA	J. Lundgren 2008, unpubl. data
	<i>Alopecosa</i> sp.	Lycosidae Araneae: Lycosidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
	<i>Pardosa</i> sp.	Araneae: Lycosidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Trochosa spinipalpis</i> Cambridge	Araneae: Lycosidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Theridion impressum</i> L. Koch.	Araneae: Theridiidae	adult	Hungary, Romania	Tóth et al. 2002; I. Grozea 2008, pers. comm.
	<i>Theridion pictum</i> Walchueter		adult	Hungary	Tóth et al. 2002
	<i>Enoplognatha latimana</i> Hippa Oksala	Araneae: Theridiidae	adult	Hungary	Tóth et al. 2002
	<i>Achaearanea tepidariorum</i> Koch.	Araneae: Theridiidae	adult	Lab	Tóth et al. 1998
	<i>Xisticus</i> sp.	Araneae: Thomisidae	adult	Romania	I. Grozea 2008, pers. comm.
	–	Chilopoda:	egg	Canada	Stoewen & Ellis 1991
	<i>Chauliognathus limbicollis</i> LeConte	Coleoptera: Cantharidae	larva	Mexico	Alvarez-Zagoya & Perez-Dominguez 2006
	–	Coleoptera: Carabidae	egg, larva	USA	Brust 1991b; Brust & House 1990; Brust et al. 1986; Best & Beegle 1977; Kirk 1982
	<i>Amara similata</i> Gyllenhal		larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Bembidion rapidum</i> LeConte		larva	USA	J. Lundgren 2008, unpubl. data
	<i>Bembidion quadrimaculatum</i> (L.)		larva	USA	J. Lundgren 2008, unpubl. data
	<i>Brachinus crepitans</i> (L.)	Coleoptera: Carabidae	larva	Hungary	J. Lundgren & S. Toepfer 2007 unpubl. data
	<i>Carabus monilis</i> F.		larva	Lab	J. Lundgren & T. Haye 2007, unpubl. data

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
	<i>Cyclotrachelus alternans</i> (Casey)	Coleoptera: Carabidae	larva	USA	J. Lundgren 2008, unpubl. data
	<i>Elaphropus nr. xanthopus</i> (Dej)	Coleoptera: Carabidae	larva	USA	J. Lundgren 2008, unpubl. data
	<i>Pseudoophonus</i> (= <i>Harpalus</i> ) <i>rufipes</i> DeGeer		larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Poecilus chalcites</i> (Say)	Coleoptera: Carabidae	larva	USA	J. Lundgren 2008, unpubl. data
	<i>Poecilus cupreus</i> L.		larva	Hungary, Lab	J. Lundgren & T. Haye 2007, unpubl. data; Medic 2007
	<i>Pterostichus anthracinus</i> Illiger		larva	Lab	J. Lundgren & T. Haye 2007, unpubl. data
	<i>Pt. melanarius</i>		larva	Lab	J. Lundgren & T. Haye 2007, unpubl. data
	<i>Scarites</i> spp.	Coleoptera: Carabidae	larva	USA	J. Lundgren 2008, unpubl. data
	<i>Trechus quadristiatus</i> (Shrank)		larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
–		Coleoptera: Coccinellidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
–		Coleoptera: Staphylinidae	egg, larva	USA	Brust 1991b; Brust & House 1990
	<i>Dysmachus cochleatus</i> (Loew)	Diptera: Asilidae	adult	Hungary	Toepfer et al. 2004
	<i>Tetramorium caespitum</i> L.	Hymenoptera: Formicidae	larva	Hungary	J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Lasius neoniger</i> Emery		egg	USA	Kirk 1981
	<i>Lasius niger</i> Americanus		adult	USA	Flint 1914

Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
	<i>Armadillidium vulgare</i> Latr.	Isopoda: Armadillidiidae	egg	Lab	B. Hibbard 2007, pers. comm.
	<i>Androlaelaps</i> sp.		egg, larva	USA	Mihm & Chiang 1976
	<i>Stratiolaelaps</i> sp.		egg, larva	USA	Mihm & Chiang 1976
	<i>Hypoaspis aculeifer</i> Canestrini	Mesostigmata: Laelapidae	egg	Canada	Stoewen & Ellis 1991
	—	Opiliones: Phalangidae	larva	USA, Hungary	J. Lundgren 2008, unpubl. data; J. Lundgren & S. Toepfer 2007, unpubl. data
	<i>Gryllus campestris</i> L.	Orthoptera: Gryllidae	larva	Hungary	S. Toepfer 2008, unpubl. data
	<i>Gryllus pennsylvanicus</i> Burmeister		larva	USA	J. Lundgren 2008, unpubl. data
	<i>Tettigonia viridissima</i> L.	Orthoptera: Tettigonidae	adult	Hungary	Toepfer et al. 2004
	<i>Chaussieria</i> sp.	Actinedida: Anystidae	larva	USA	J. Lundgren 2008, unpubl. data
<i>D. viridula</i> (F.)	—	Hemiptera: Reduviidae	adult	Mexico	Eben & Barbercheck 1996
<i>D. vittata</i>	<i>Ph. pennsylvanica</i>		adult	USA	Badulf 1939
<i>Diabrotica</i> spp.	—	Acarina: Ameroseiidae	egg	USA	Mihm & Chiang 1976; Stoewen & Ellis 1991
	<i>Rhodacarellus</i> sp.	Acarina: Rhodacaridae	egg, larva	Lab, USA	Chiang 1970
	<i>Stratiolaelaps</i> sp.		egg, larva	Lab, USA	Chiang 1970



Table 4 (Continued)

Host	Predator	Order: Family	Stage attacked	Location	Reference
	<i>Chauliognathis marginatus</i> (F.)	Coleoptera: Cantharidae	–	USA	Branson et al. 1982
	<i>Pheidole</i> sp.		egg	Costa Rica and Lab	Risch 1981
	<i>Solenopsis geminata</i> F.		egg	Costa Rica and Lab	Risch 1981
	<i>Harpalus erraticus</i> Say	Coleoptera: Staphilinidae	adult	Lab	Kirk 1973a,b ; 1974
	<i>Dalotia</i> (= <i>Atheta</i> ) <i>coriaria</i> (Kraatz)		eggs, larva	Lab	B. Hibbard, Larry Watrous 2007, pers. comm.
	<i>Ph. Bicarinata longula</i>		–	USA	Ballard & Mayo 1979

(McCartney and Stinner, unpublished data in Stinner and House 1990). One of the best studied systems in this regard is predation of *D. undecimpunctata howardi* by *Tyrophagus putrescentiae*. These mites consume *D. undecimpunctata* eggs in the field and laboratory, successfully detecting eggs from up to 8 cm away (Brust and House 1988).

Other work on predation by mites has shown that in the Midwestern USA, manure applications to maize fields significantly increased endemic predatory mite populations (Mihm 1972). Simultaneously, populations of *D. virgifera* and *D. longicornis* in manure-treated fields were reduced to about 50% of those in control fields, suggesting that predaceous mites may play a role in reducing *Diabrotica* populations. This trophic relationship is further evidenced by the observation that laelapid mites readily prey on *Diabrotica* eggs and larvae in the laboratory (Chiang 1970). In another study, however, enhancement of mite populations via manure applications had little effect on *D. v. virgifera* populations in the field (Allee and Davis 1996). Additional work is needed on the factors influencing the abundance and efficacy of mites in biological control.

Finally, some trombidid and anystid mites are also *Diabroticina* predators. At least three species of ectoparasitic immature trombidid mites have been found attacking larvae of *C. trifurcata* and *D. speciosa* (Peterson, Smelser, Klubertanz, Pedigo, and Welbourn 1992; G. Cabrera Walsh 1998, unpublished data), but their influence on *Diabroticina* populations remains unknown. J. Lundgren (unpublished data) found that the anystid mite *Chaussieria* sp. and an unidentified trombidid mite were frequent predators of *D. v. virgifera* larvae and eggs in midwestern USA maize fields.

Ants are dominant predators of arthropods in many habitats and geographical regions, helping to control insect pests in many cases (Paulson and Akre 1992). Although ants are known predators of *Diabrotica* spp., the application of these predators as biological control agents of *Diabrotica* in cropland has not been attempted. *Lasius neoniger* Emery (Hymenoptera: Formicidae) significantly reduced *Diabrotica* spp. larval populations in South Dakota, USA, presumably by direct feeding on immature stages (Kirk 1981); although *L. neoniger* did not eat *D. v. virgifera* eggs in laboratory trials (Ballard and Mayo 1979). Risch (1981) demonstrated that other ant species may have a significant impact on *Diabrotica* egg abundance. In field experiments in Costa Rica, *Solenopsis geminata* F. and *Pheidole* sp. (Hym.: Formicidae) removed 80% of exposed *Diabrotica* eggs within 3 days (Risch 1981). In Hungarian maize fields, *Tetramorium caespitum* L. (Hym.: Formicidae) was frequently observed to consume exposed larvae of *D. v. virgifera*, attacking up to 50% of tethered larvae within 1 h of their placement in the field (Lundgren and Toepfer, unpublished data). As common predators in agricultural settings worldwide, ants are quick to exploit *Diabroticina* prey if available.

Carabids are among the most abundant generalist predators in croplands in temperate climates (Lovei and Sunderland 1996; Lundgren et al. 2006), and constitute the third group of *Diabrotica* predators that has received appreciable attention in predation studies. More than 24 species of carabids have been shown to feed on *Diabrotica* in the laboratory or in the field (Table 4). Within the rootworm-associated predator community in South Dakota, USA, rootworm DNA was found in the guts of captured *Poecilus chalcites* and *Scarites quadriceps* in high proportions (18 and 20% of the carabid populations, respectively). Snyder and Wise (1999, 2000)

and Williams, Snyder, and Wise (2001) documented that predatory carabids and spiders are able to reduce populations of *D. u. howardi* by as much as 50% in small vegetable plots.

Other arthropod predators seem to be less implicated in feeding on Diabroticina pest populations (e.g. Kirk 1982). Two studies concluded that predators contributed little mortality to *Diabrotica* eggs under field conditions (Dominique and Yule 1984; Stoewen and Ellis 1991). Toth, Horvath, Komaromi, Kiss, and Szell (2002) found 12 spider families present in maize fields when adult *D. v. virgifera* were present, and that adult *D. v. virgifera* are captured in webs of *Theridion* spp. (Araneae: Theridiidae) and *Agelena* spp. (Araneae: Agelinidae). However, the densities of these spiders were low and presumably so were the predation pressures they exerted on *D. v. virgifera* adults. Larval predation by epigeal wandering spiders such as lycosids may prove to be more important to *Diabrotica* population dynamics (Lundgren et al., in press)

### *Arthropod parasitoids*

Parasitoids have been the most common type of natural enemy introduced for biological control of insect pests (Greathead 1976). In general, beetle larvae in the subfamily Galerucinae are parasitized by the hymenopteran families Encyrtidae, Eulophidae, Braconidae as well as by the dipteran Tachinidae (Cox 1994; Jolivet, Cox, and Petitpierre 1994). Adult Galerucinae are parasitized by braconids in the subfamily Euphorinae and tachinids in the tribe Blondeliini (Jolivet et al. 1994). Studies of parasitoids of adult Diabroticina are rare, and to date there are no known parasitoids of their immature stages (Javier and Peralta 1975; Kuhlmann 1998; Toepfer et al. 2008b). In Europe, no parasitoids have been found in association with any life stage of the invasive *D. v. virgifera* (Toepfer and Kuhlmann 2004).

In the New World, Diabroticina are hosts to at least four species in the genus *Celatoria* (Diptera: Tachinidae, Blondeliini) (Table 5), all of which are primary solitary endoparasitoids of adult beetles (Bussart 1937; Fischer 1983; Zhang, Toepfer, Riley, and Kuhlmann 2004). After completing larval development, the parasitoid larva leaves the beetle and forms a puparium on a nearby plant or on the soil surface (Bussart 1937). The larvae of *C. setosa* and *C. bosqi*, hibernate in the host tissue of the *Diabrotica* adults (Fischer 1983; Cabrera Walsh 2004), however, the hibernation behaviour of other *Celatoria* species is unknown. All *Celatoria* species can have several generations a year (Bussart 1937; Gould 1944; Cabrera Walsh 2004).

The South American *Celatoria bosqi* Blanchard was originally described from *D. speciosa* (Blanchard 1937). Since then, it has been collected from *D. speciosa* (up to 18% parasitism), sporadically from *D. viridula* (F.) and once in *Hystiopsis* sp. (Diabroticina: Cerotomites) (Cabrera Walsh 2004). Although there is a record of *C. bosqi* from adult *Cerotoma arcuata* Olivier (= *Andrector arcuatus*) (Magalhães and Quintela 1987), extensive surveys in South America never yielded any such cases (Cabrera Walsh 2004; Dequech et al. 2006), suggesting that the parasitoid reported by Magalhães and Quintela (1987) was not *C. bosqi*. In laboratory host-range tests, *C. bosqi* did not attack any *virgifera* group members, but readily parasitized *D. speciosa* (*fucata* group) (Cabrera Walsh 2004).

The Mexican species *Celatoria compressa* (Wulp) has been collected from many species in the genera *Acalymma* and *Diabrotica*, the latter including five species in the

Table 5. Records of arthropod parasitoids successfully parasitizing species in the subtribe Diabroticina (Coleoptera: Chrysomelidae).

Host	Parasitoid	Order: Family	Stage attacked	Location	Reference
<i>Acalymma bivittula</i> (Kirsch)	<i>Centistes gasseni</i> Shaw	Hymenoptera: Braconidae	adult	Brazil	Cabrera Walsh et al. 2003
<i>A. blandula</i> LeConte	<i>Celatoria setosa</i> (Coquillett) ( <i>Celatoria diabroticae</i> (Shimer))***	Diptera: Tachinidae	adult	USA	Fischer 1983
		Diptera: Tachinidae	adult	Lab	(Fischer 1983)***
<i>A. blomorum</i> Munroe Smith	<i>Celatoria compressa</i> (Wulp)	Diptera: Tachinidae	adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>A. fairmairei</i> (F.)	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>A. innubum</i> (F.)	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>A. trivittatum</i> (= <i>trivittata</i> ) (Mannerheim)	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996
	( <i>Cel. diabroticae</i> )**		adult	USA	(Essig 1926; Arnaud 1978)**
	( <i>Cel. diabroticae</i> )***		adult	Lab	(Fischer 1983)***
	<i>Cel. setosa</i>		adult	USA, Mexico	Fischer 1983; R. Alvarez & S. Toepfer 2002, unpubl. data
<i>A. vittatum</i> (= <i>vittata</i> ) (= <i>D. melanocephala</i> ) (F.)	( <i>Cel. diabroticae</i> )**		adult	USA	(Walton 1914; Lowry 1918; Chittenden 1919; Bussart 1937; Fattig 1949; Arnaud 1978)**
	( <i>Cel. diabroticae</i> )***		adult	Lab	(Fischer 1983)***
	<i>Cel. setosa</i>		adult	USA	Chittenden 1919; Houser & Balduf 1925; Bussart 1937; Gould 1944; Arnaud 1978; Fischer 1981; Elsey 1988a,b; R. Smyth, 1999, unpubl. data

Table 5 (Continued)

Host	Parasitoid	Order: Family	Stage attacked	Location	Reference
	<i>Centistes diabroticae</i> (Gahan)	Hymenoptera: Braconidae	adult	USA	Gahan 1922; Houser & Bal- duf 1925; Marsh 1979; Krombein et al. 1979; Fischer 1981, R. Smyth, 1999, un- publ. data
<i>Aulacophora foveicollis</i> Lucas *	<i>Cen. gasseni</i> <i>Cel. compressa</i>		adult adult	Lab Lab	Schroeder & Athanas, 2002 Kuhlmann et al. 2005
<i>Cerotoma arcuata</i> Olivier (= <i>Andrector arcuatus</i> )	( <i>Celatoria bosqi</i> Blanchard)**	Diptera: Tachinidae	adult	Brazil	(Magalhães & Quintela 1987)**
	Unidentified <i>Strongygaster</i> sp. Macquart	Diptera: Tachinidae	adult	Brazil	Micheli 2005
<i>C. atrofasciata</i> Jacoby	<i>Cel. compressa</i>		adult	Mexico	Gámez – Virues & Eben 2005
<i>C. trifurcata</i> (Foerster)	( <i>Cel. diabroticae</i> )**		adult	USA	(McConnell 1915, Eddy & Nettles 1930; Isely 1930; Fronk 1950; Herzog 1977; Marrone et al. 1983)** (Fischer 1983)***
	( <i>Cel. diabroticae</i> )***		adult	Lab	
	Undescribed <i>Celatoria</i> sp.	Diptera: Tachinidae	adult	USA	Danielson et al. 2000
	Undescribed <i>Medina</i> sp. (near <i>quinteri</i> )****	Diptera: Tachinidae	adult	USA	Loughran & Ragsdale 1986****
	<i>Strongygaster</i> (= <i>Hyalomyodes</i> ) <i>triangulifer</i> (Loew)	Diptera: Tachinidae	adult	USA	Herzog 1977.
<i>D. amecameca</i> Krysan & Smith	<i>Cel. compressa</i>		adult	Mexico	Eben 2002

Table 5 (Continued)

Host	Parasitoid	Order: Family	Stage attacked	Location	Reference
<i>D. balteata</i> LeConte	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005; Alvarez-Zagoya & Perez-Dominguez 2006
	<i>Cel. diabroticae</i>		adult	Lab	D. Weber, B. Kurtz, S. Toepfer 2006, unpubl. data; Fischer 1983***
	<i>Cen. Diabroticae</i>		adult	Mexico	I. Hiltbold & S. Toepfer 2006, unpubl. data
<i>D. barberi</i> Smith	<i>Cen. Gasseni</i>		adult	Lab	Schroeder & Athanas, 2002
Lawrence	<i>Cel. diabroticae</i> .		adult	USA	Prischmann & Dashiell 2008 subm.
<i>D. cristata</i> (Harris)	( <i>Cel. diabroticae</i> ) ***		adult	Lab	(Fischer 1983)***
<i>D. limitata</i> (Sahlberg)	Undescribed <i>Celatoria</i> nov. sp.	Diptera: Tachinidae	adult	ArgentinaBrazil	G. Cabrera Walsh 2001, unpubl. data
	<i>Cen. Gasseni</i>		adult	ArgentinaBrazil	Cabrera Walsh et al. 2003.
<i>D. longicornis</i> (Say)	<i>Cel. diabroticae</i>		adult	USA	Fischer 1983
<i>D. porracea</i> Harold	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>D. scutellata</i> Baly	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>D. sexmaculata</i> Baly	<i>Cel. compressa</i>		adult	Mexico	Gámez – Virues & Eben 2005
<i>D. speciosa</i> (Germar)	<i>Cel. bosqi</i>		adult	Argentina Bolivia, Brazil, Paraguay, Uruguay	Blanchard 1937; Christensen 1943; Parker et al. 1953; D'Araujo e Silva et al. 1967; Gassen 1989, 1993; Salles 1996; Heineck-Leonel & Salles 1997; Cabrera Walsh 2003, 2004; Dequech 2006

Table 5 (Continued)

Host	Parasitoid	Order: Family	Stage attacked	Location	Reference
	<i>Cen. Gasseni</i>		adult	Argentina Brazil, Paraguay	Heineck-Leonel & Salles 1997; Schroder & Athanas 2002; Cabrera Walsh et al. 2003.
<i>D. tibialis</i> Jacoby	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996; Gámez – Virues & Eben 2005
<i>D. u. howardi</i> Barber	<i>Cel. diabroticae</i>		adult	USA	Sell 1915; Fronk 1950; Sum- mers & Stafford 1953; Ar- naud 1978; Fischer 1983; Gordon et al. 1987; Meinke & Gould 1987; Elsey 1988a,b; Luginbill 1940; Isely 1929; Sweetman 1926; Arrant 1929; D. Weber 2006, unpubl. data.
	( <i>Cel. setosa</i> )**		adult	USA	(Fattig 1949; Fischer 1981)**
	<i>Cen. Gasseni</i>		adult	Lab	Schroeder & Athanas, 2002
<i>D. u. undecimpunctata</i> Mannerheim	<i>Cel. diabroticae</i>		adult	USA	Michelbacher et al. 1943, 1955; Rockwood & Ragsdale 1943; Arnaud 1978; Fischer 1981
	( <i>Cel. setosa</i> )**		adult	USA	(Bussart 1937; Fischer 1981)**
	( <i>Myiopharus</i> ( = <i>Pseudomyothyria</i> ) <i>ancillus</i> Walker)**	Diptera: Tachinidae	adult	USA	(Brauer & Bergenstamm 1895; Arnaud 1978)**
<i>D. v. virgifera</i> LeConte	<i>Cel. compressa</i>		adult	Mexico	Alvarez-Zagoya & Perez-Dominguez 2006
	<i>Cel. diabroticae</i>		adult	USA	Fischer 1983

Table 5 (Continued)

Host	Parasitoid	Order: Family	Stage attacked	Location	Reference
	<i>Cen. Diabroticae</i>		adult	Lab	B. Kurtz & S. Toepfer 2005, unpubl. data
	<i>Cen. Gasseni</i>		adult	Lab	Schroeder & Athanas 2002
<i>D. v. zae</i> Krysan & Smith	<i>Cel. compressa</i>		adult	Mexico	A. Eben and R. Alvarez 2001, unpubl. data
	<i>Cen. Diabroticae</i>		adult	Mexico	I. Hiltbold & S. Toepfer 2006, unpubl. data
<i>D. viridula</i> (F.)	<i>Cel. compressa</i>		adult	Mexico	Eben & Barbercheck 1996
	<i>Cel. bosqi</i>		adult	Argentina	Cabrera Walsh 2003, 2004
	<i>Cen. Gasseni</i>		adult	Argentina, Brazil, Paraguay	Cabrera Walsh et al. 2003.
<i>Gynandrobrotica lepida</i> (Say)	<i>Cel. compressa</i>		adult	Mexico	A. Eben 2002, unpubl. data
<i>G. nigrofasciata</i> (Say)	<i>Cel. compressa</i>		adult	Mexico	Gámez – Virues & Eben 2005
<i>Hystiopsis</i> sp.	<i>Cel. bosqi</i>		adult	Argentina	Cabrera Walsh 2004
Unknown	<i>Celatoria maracasi</i> Thompson	Diptera: Tachinidae	unknown	Trinidad	Thompson 1968

\* belongs to subtribe Aulacophorina which is closely related to Diabroticina

() \*\* citations that were not verified by ensuing surveys or by host range tests

() \*\*\* tachinid larvae did not attack this host in laboratory assays, but developed successfully when the host was artificially inoculated

\*\*\*\* possibly similar to the undescribed *Celatoria* sp. of Danielson (2000)



*virgifera* group and five species in the *fucata* group (Eben and Barbercheck 1996; Gámez-Virués and Eben 2005; Alvarez-Zagoya and Perez-Dominguez 2006) (Table 5). Two species of *Gynandrobrotica* (Diabroticina: Diabroticites), as well as *Cerotoma atrofasciata* Jacoby (Diabroticina: Cerotomites) are also known hosts. In these hosts, parasitism levels as high as 10–16% have been observed (Eben and Barbercheck 1996; Eben 2002; Gámez-Virués and Eben 2005) (Table 5). In laboratory host-range tests, *C. compressa* parasitized and developed from *D. v. virgifera* and *D. balteata*, and occasionally from *Aulacophora foveicollis* Lucas (Chrysomelidae, Galerucinae, Luperini, Subtribe Aulacophorina) (Kuhlmann, Toepfer, and Zhang 2005), which is a pumpkin pest from northwest Asia and southeast Europe (Anonymous 2007). In the same study, *C. compressa* did not attack any of the six other chrysomelid species outside the Diabroticina offered.

The North American *Celatoria diabroticae* (Shimer) was originally described in the genus *Tachina* by Shimer in 1871. High levels of parasitism (up to 20%) by *C. diabroticae* have been reported in the USA from *Diabrotica undecimpunctata howardi* Barber (Summers and Stafford 1953; Fischer 1981) and *D. u. undecimpunctata* Mannerheim (Fischer 1983) (Table 5). *Celatoria diabroticae* parasitizes *Diabrotica longicornis* (Say) (Fischer 1983) and *D. v. virgifera* (Fischer 1981, 1983) at lower rates. In laboratory host-range tests, *C. diabroticae* readily parasitized and developed from *Diabrotica* species of both the *fucata* and *virgifera* groups (Fischer 1983). Field records of *C. diabroticae* from species within the genus *Acalymma*, e.g. in *A. trivittata* (Shimer 1871; Arnaud 1978) and *A. vittatum* (= *A. or D. vittata*, or = *D. melanocephala*) (F.) (Bussart 1937; Arnaud 1978) were neither confirmed in later field surveys nor in laboratory host-range tests (Fischer 1983). McConnell (1915) reported *C. diabroticae* from *Cerotoma trifurcata* without describing how the parasitoid was identified (Fischer 1983). Subsequent research, i.e. Eddy and Nettles (1930); Isely (1930); Fronk (1950); Herzog (1977); Arnaud (1978); and Marrone et al. (1983), was based on McConnell's dubious identification (1915). Since *C. diabroticae* did not attack *Cerotoma trifurcata* in the lab, these reports may be incorrect and *Cerotoma* species may not be hosts of *C. diabroticae* (Fischer 1983). The observed parasitoid remains unidentified (Danielson, Brandle, and Hodges 2000), but may be related to *Medina* sp. near *quinteri*, which causes parasitism levels of up to 40% in *C. trifurcata* in Minnesota, USA (Loughran and Ragsdale 1986; D.M. Wood, personal communication, 2007).

The North American *Celatoria setosa* (Coquillett) was originally described by Coquillett (1890, 1895) as *Chaetophleps setosa* and later by Walton (1914) as *Neocelatoria ferox*. Field records in the USA and Mexico as well as laboratory host-range tests indicate that *C. setosa* exclusively parasitizes *Acalymma* species, such as *A. blandula* LeConte, *A. trivittata* (Mannerheim) and *A. vittatum* (F.) (Bussart 1937; Arnaud 1978; Fischer 1983; Elsey 1988a,b) (Table 5). Although there are sporadic records of *C. setosa* from *D. u. undecimpunctata* and *D. u. howardi* in the USA (Bussart 1937; Arnaud 1978; Elsey 1988a,b), *C. setosa* has never successfully parasitized and developed from beetles offered in any genus (including *Diabrotica*) other than *Acalymma* (Fischer 1983).

Adult Diabroticina also host at least two species in the parasitoid genus *Centistes* (Hymenoptera: Braconidae, Euphorinae) (Table 5). *Centistes* species are solitary koinobiont endoparasitoids of adult beetles, particularly in the families Curculionidae, Chrysomelidae, Coccinellidae, Anthicidae, and Carabidae (Loan 1964, 1972;

Shaw 1985). *Centistes* species deposit single eggs into the thorax of adult beetles, puncturing one of the sutures near the base of the elytra. The mature parasitoid larva emerges from the host and pupates inside a tightly woven silk cocoon (Gahan 1922).

The North American *Centistes diabroticae* (Gahan) was originally described as *Syrrhizius diabroticae* by Gahan (1922). It has been collected from *A. vittatum* in Mexico and the USA (Gahan 1922; Krombein, Hurd, Smith, and Burks 1979; Fischer 1981; R. Smyth 1999, unpublished data) as well as from *D. v. zeae* and *D. balteata* in Mexico (I. Hiltbold and S. Toepfer 2006, unpublished data). Parasitism rates of up to 23% in the USA and up to 8% in Mexico were reported.

The South American *Centistes gasseni* Shaw was originally described from *D. speciosa* (Shaw 1995). It is known to parasitize adults of three *Diabrotica* species in northeastern Argentina, eastern Paraguay and southern Brazil: *D. speciosa* (*fucata* group) (2% mean parasitism), *D. viridula* (*virgifera* group) (1.2%), and *D. limitata* (*fucata* group) (7.5%). A single *C. gasseni* emerged from among 3960 *Acalymma bivittula* (Kirsch) collected within the parasitoid's geographical range (Cabrera Walsh, Athanas, Salles, and Schroder 2003); *A. bivittula* is thus considered an accidental host. In laboratory host-range tests, *C. gasseni* parasitized and developed in three North American *Diabrotica* species and in *A. vittatum* (Table 5), but ignored *C. trifurcata* (Schroder and Athanas 2002). The hyperparasitoid *Mesochorus* sp. (Hymenoptera: Ichneumonidae) was reported from *C. gasseni* cocoons in Argentina (Cabrera Walsh 2003).

Occasionally, dipteran Phoridae become facultative parasitoids of Diabroticina in crowded laboratory cultures (R.H.L. Disney, personal communication, 2005). *Megaselia scalaris* (Loew) (Diptera: Phoridae) have been reported from adult *D. v. virgifera* (R. Alvarez and J. Miall, personal communication, 2005), and *Phalacrotophora* sp. (near *P. nedae* (Mall.)) and *P. epeirae* (Brues) from pupae and larvae of *D. balteata* (Saba 1970). However, these phorids are primarily polyphagous saprophagous species and are not considered to be potential biological control agents.

### Miscellaneous

Vertebrate predators may be important biological controls for herbivorous insects in some agroecosystems (Schmitz et al. 2000; Williams-Guillén, Perfect, and Vandermeer 2008). A number of vertebrate predators, predominantly birds, have been shown to prey on *Diabrotica* spp. in North America (Webster 1913a,b). The red-winged blackbird *Agelaius phoeniceus* L. (Passeriformes: Icteridae) frequently preys on *D. longicornis* in Canada (Bollinger and Caslick 1985a,b). Gould and Massey (1984) found that two species of toads, *Bufo* spp. (Amphibia: Bufonidae) as well as the deer mouse, *Peromyscus maniculatus* Wagner (Mammalia: Muridae) and bobwhite quail, *Colinus virginianus* (Galliformes: Odontophoridae) readily consumed adult *D. u. howardi* under laboratory conditions.

The sticky seed heads of *Setaria verticillata* (L.) P.B. (Poaceae) were found to trap up to 30 *D. v. virgifera* beetles per head in maize fields in Hungary (Toepfer and Kuhlmann 2004).

### Action and research needs for sustainable management of Diabroticina pests

The evolution and spread of resistance of Diabroticina to insecticides and crop rotation, the invasion of *D. v. virgifera* into Europe, and the recent large-scale deployment of Diabrotica-active Bt maize in North America have converged to generate a sense of urgency for developing biological control options against Diabroticina pest species. To date, biological control strategies including inundative or classical biological control were not considered potentially competitive with control achieved by insecticides, crop rotation or transgenic maize, because little was known about natural enemies of Diabroticina by academics, growers and industry. To address the above concerns, legislators and other decision-makers are advised to support development of biological control options, and are, particularly in Europe, encouraged to connect the existing subsidy of maize production with a requirement for integrated or organic farming.

Taking the above-reviewed studies into account, here we prioritize action and research needs for the following biological control options of Diabroticina pests.

#### Inundative biological control

The periodic application of biological control products, such as formulations with bacteria, fungi, viruses or nematodes – has considerable potential. In research, organisms like nematodes or fungi that have already been commercialised should be emphasized. Species of both nematodes and fungi are already registered for use against soil dwelling beetle pests in many countries (Babendreier et al. 2006), making them more feasible research subjects than the poorly studied protista, microsporidia, viruses and bacteria. Key factors behind the success or failure of entomopathogenic nematodes or fungi in pest control still need to be investigated:

- a. The development of biological control products using heterorhabditid and steinernematid nematodes against a wide range of Diabroticina larvae is facilitated by the increasing number of commercially mass-produced nematode species and strains (Ehlers 2001). Critical interactions between field crop, soil, beetle larvae and nematodes must be understood for soil dwelling Diabroticina, like *D. v. virgifera*, *D. u. undecimpunctata*, *D. u. howardi* or *D. balteata*. For example, the influence of soil structure and composition on nematode movement, orientation and persistence warrants detailed investigation. Further, nematode application techniques need to be optimised, as knowledge of the large-scale use of nematodes in field crops is limited (Cabanillas et al. 2005). Means by which nematode population levels are maintained during critical periods should be investigated. For example, how nematodes persist during periods of host absence or environmental extremes should be elucidated; nematodes may require non-target hosts of optimal size and population density in the soil. Finally, nematode strains could be selected for propagation, locomotion through the soil, host virulence, and ability to locate the host plant (Barbercheck et al. 2003; T. Turlings, personal communication, 2007). Being short-lived and highly fecund, nematodes are feasible candidates for such selective breeding.
- b. Entomopathogenic fungi may have potential in biological control of both Diabroticina adults and larvae. Little is known about fungi outside the genera

*Beauveria* and *Metarhizium* with regards to *Diabroticina* control. But strains in both genera that are highly virulent to *Diabroticina* may allow the development of biological control products. Commercial fungal formulations are already widely and successfully used against many soil dwelling pests, including: *Metarhizium anisopliae* against *Amphimallon* spp., the garden chafer *Phyllopertha horticola* L. (Coleoptera: Scarabaeidae), and the vine weevil *Otiorhynchus sulcatus* (F.) (Col.: Curculionidae); and *Beauveria brongniartii* against *Melolontha* spp. (Col.: Scarabaeidae) (Keller 2004; Strasser et al. 2006; Keller and Schweizer 2007). Isolates may exist which show adaptations, such as partial or complete specificity, to *Diabroticina*, and molecular techniques could prove valuable in distinguishing these (Schwarzenbach, Widmer, and Enkerli 2007). Commercial formulations for pest control need to be optimized for long-term storage which can be achieved with many isolates of *Beauveria* and *Metarhizium* spp., and efficient application techniques developed, such as seed coating, water dispersable powders, granules, baits, and auto-dissemination methods. Furthermore, the ecology of entomopathogenic fungi in the soil is still poorly understood, including the phenomena of endophytism, host repellence, seasonal persistence, and rhizosphere interactions. Ecological studies may also elucidate the influence of management practices on indigenous fungi in agro-ecosystems.

Although a lower priority than nematode and fungal products, further exploration of the occurrence and ecology of other microbials in *Diabroticina* may reveal potential for biological control options. Although transgenic *Bt* maize is widely used, no conventionally formulated bacteria-based products are used against *Diabroticina* pests in field crops. Future bacterial research should focus on the isolation and characterization of indigenous *Bt* strains with specific activity against *Diabroticina* pest species. *Bacillus thuringiensis* strains may be isolated from soils and characterized using degenerative PCR primer sets specific for various *Cry* gene families (Bravo et al. 1998; Uribe, Martinez, and Ceron 2005). *Cry34* and *Cry35* proteins have shown high activity against larvae of *Diabrotica* species, but toxicity tests of conventional *Bt* products based on *Cry34* and *Cry35* are still lacking. Furthermore, application strategies for using conventional *Bt* products against soil dwelling *Diabrotica* larvae do not exist, and it is still questionable how larvae could be brought to feed on *Bt* in the soil. Models exist from other systems and should be explored, including *B. thuringiensis japonicum* against *Popillia japonica* Newman (Coleoptera: Scarabaeidae), and *Serratia entomophila* Grimont (Proteobacteria: Enterobacteriaceae) against *Costelytra zealandica* White (Coleoptera: Scarabaeidae). Some Rickettsiaceae may also show potential for control of *Diabrotica* species (Floate et al. 2006). The rapid expansion of *Wolbachia* research may offer new directions for the study of population dynamics of *Diabroticina* pests (Giordano et al. 1997; Floate et al. 2006). The development of molecular screening of *Diabroticina* guts may identify promising new bacteria species. Protista and microsporidia in the *Diabroticina* also require further exploration, as some of these pathogens have been successfully used for control of other pests. For example the grasshopper pathogen *Paranosema* (= *Nosema*) *locustae* Canning (Microsporidia) is registered and commercially available for biological control (Lacey et al. 2001; Copping 2004).

although it tends to act as a chronic agent of control of populations over time, rather than as a quick acting control of a pest outbreak.

Baculoviridae offer the greatest potential among viruses for development of microbial-based insecticides; Nucleopolyhedroviruses and Granuloviruses ought to be surveyed in Diabroticina pests in their American areas of origin (Miller et al. 1999). Techniques from existing successful biological control systems may be adopted. Examples include the use of the *Helicoverpa zea* – nucleopolyhedrovirus against lepidopteran pests *Heliothis* spp. and *Helicoverpa* spp. (Copping 2004), and the augmentative control of Rhinoceros beetles using *Oryctes* viruses (Huger 2005).

Currently, little research is being conducted to explore the use of botanicals or other natural source insecticides against Diabroticina beetles. Cassia Andrade dos Santos Seffrin (2006) found that aqueous extracts from the Meliaceae were anti-feedant but not fatal to *D. speciosa*. The tested extracts were refined from the following plants: *Cabralea canjerana* (Vell.) Mart., *Cedrela fissilis* Vell., *Melia azedarach* L. (var. *azedarach*), *Trichilia catigua* A. Juss., *T. clausenii* C. DC. and *T. elegans* A. Juss. (all Meliaceae). Seed meals from *Brassica carinata* and *Eruca sativa* (both Brassicaceae) that emit insecticidal volatiles were shown to kill the soil-living pest larvae of *Agriotes* spp. (Coleoptera: Elateridae) in maize (Furlan et al. 2004), however, their wider environmental impact has yet to be evaluated.

Environmentally friendly attract–dissemination–kill methods against adult Diabroticina are promising management options, because several semiochemicals are known to attract Diabroticina (Guss et al. 1982, 1984; Metcalf 1994; Chandler, Sutter, Hammack, and Woodson 1995; Metcalf, Lampman, and Deem 1995; Hammack, Hibbard, Holyoke, Kline, and Leva 1999). Attractive semiochemicals like sex pheromones, floral baits or feeding stimulants of certain Diabroticina (Hesler and Sutter 1993; Hoffmann, Kirkwyland, Smith, and Long 1996; Cabrera Walsh and Cabrera 2004; Cabrera Walsh, Weber, Mattioli, and Heck 2008) could be laced with pathogens that would kill adult beetles (Levine and Oloumi-Sadeghi 1991). Most Diabroticina have a strong craving for cucurbitacins, bitter triterpenoids that function as plant chemical defences, primarily in the family Cucurbitaceae (Contardi 1939; Howe, Sanborn, and Rhodes 1976; Metcalf and Lampman 1989). Toxic baits containing cucurbitacin-rich juices or powders are commercially available under at least five brand names and several formulations (Behle 2001; Chandler 2003). Moreover, these baits have shown no negative impact on non-target arthropods (Ellsbury, Gaggero, and Johnson 1996a; McKenzie et al. 2002), making them compatible with other biocontrol programmes (Lewis, Gunnarson, and Robbins 2005). The results obtained with the application of these baits laced with insecticides to control *D. v. virgifera* and *D. barberi* have been variable and not always favourable (Chandler 2003; Gerber et al. 2005; French, Chandler, and Riedell 2007). Three explanations have been proposed for these irregular results: resistance to toxicants (Parimi et al. 2003), inadequate residual activity of the bait (Gerber et al. 2005), and a distinct male bias in response of Diabroticina to cucurbitacin sources (Cabrera Walsh 2003; Cabrera Walsh and Cabrera 2004; Cabrera Walsh et al. 2008). These three factors indicate that current formulations need further improvements to serve as effective pest management tools.

Mating disruption and mass trapping methods based on semiochemicals and sex pheromones have so far not succeeded, and may prove uneconomical at least for field crops. The attempt by Wennemann and Hummel (2001) to disrupt mating of *D. v.*

*virgifera* was unsuccessful, probably because most Diabroticina beetles are active, long-lived and males can mate multiple times. However, management of *Acalymma vittatum* using its potent male-produced aggregation pheromone (Smyth and Hoffmann 2003; Morris et al. 2005) early in the growing season when crop damage is most likely, may be feasible in high-value crops, if an economical synthesis can be devised.

Larval disruption methods could be considered for soil dwelling Diabroticina pests. For example, larvae may be attracted to CO<sub>2</sub> sources away from roots, interrupting maize location and resulting in larval starvation as suggested by Bjostad and Hibbard (1992); Bernklau and Bjostad (1998); Bernklau, Fromm, and Bjostad (2004).

### **Classical biological control**

Classical biological control should be considered in Europe and in North America against the invasive *D. v. virgifera* (Kuhlmann and van der Burgt 1989; Kuhlmann et al. 2005) by inoculative release of host-specific natural enemies of Diabroticina beetles, such as parasitoids or viruses, bacteria and other pathogens, from the beetle's areas of origin in Mexico and surrounding countries (Krysan and Smith 1987). Successful introduction and establishment of exotic natural enemies is well documented for other biological control programmes (Waage and Hassell 1982), and could provide long-term reduction in *D. v. virgifera* damage on a regional scale. In Central America, *D. v. virgifera* is attacked by a complex of natural enemies, some of which appear to be well adapted to attack *Diabrotica* and related species (Kuhlmann and van der Burgt 1998). Parasitoids like *Celatoria diabroticae*, *Centistes diabroticae* and *C. gasseni* and, with some limitations also *Celatoria compressa*, are possible candidates for classical biological control of *D. v. virgifera* in Europe; and *C. compressa*, *C. bosqi* and *C. gasseni* are possible agents for neoclassical biological control in the USA. Further host-range testing is needed to estimate the safety and efficacy of such agents (Kuhlmann et al. 2005), and hibernation strategies need to be clarified to evaluate climate compatibility (Zhang, Toepfer, and Kuhlmann 2004).

Microbials like viruses or bacteria are often host-specific and may have potential as classical biological control agents, but remain largely unexplored. Natural enemies of the soil living stages of many *Diabrotica* pests also have yet to be explored. Surveys of Diabroticina in northwestern South America and of immatures throughout temperate zones of the New World are needed. The latter is particularly crucial since pests introduced from subtropical climates to temperate ones often better adapt to the new cooler environment than do their natural enemies (see *Leptinotarsa undecimlineata* (Say) in O'Neil et al. 2005).

### **Conservation biological control**

The conservation and enhancement of natural enemies may reduce pest damage on a local scale. This option is generally promoted by guidelines and legislation for IPM or organic production worldwide; and particularly applied in Europe and the USA. Although numerous predators of *Diabrotica* spp. have been identified, their impact on beetle population dynamics remains largely unknown. Recent studies strongly suggest that predators are pivotal in reducing rootworm pressure on crops, but

further substantiation by empirical studies is needed. Next to predators, the tachinid parasitoids *Celatoria setosa* and *Celatoria diabroticae* and the braconid *Centistes diabroticae* may also emerge as candidates for biological control of Diabroticina pest species in North America (Toepfer et al. 2008b). The tachinid *Celatoria bosqi* is a candidate for biological control against *fucata* group *Diabrotica* in South America (Cabrera Walsh 2004). The enhancement of natural enemies through cultural practises such as reduced tillage, reduced weed control (Brust 1991a,b,c), cover crops, crop rotations, and soil amendments are still poorly understood.

Life table analysis under different cultural practises could help to identify practise-related biotic mortality factors in the area of origin of Diabroticina beetles (Toepfer and Kuhlmann 2006). These could be compared with life table analysis from areas where Diabroticina are invasive to elucidate the differences in mortality factors and population dynamics. Once key natural enemies or natural mortality factors are identified, cultural practises could be adapted to maximize predation or natural mortality factors in an economically feasible way.

## Conclusion

Natural enemies will be useful elements of a strategic approach to the control of Diabroticina pests. Although biological control is unlikely to compete with transgenic crops in conventional maize production, an integrated pest management strategy is likely to incorporate pest-monitoring systems, application of biological control products, classical releases of biological control agents, crop rotation, and modification of cultural techniques to enhance the natural enemy populations. Overall, there is good evidence that accelerated exploration of biological control options may provide the advances in Diabroticina pest management we urgently need.

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